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Annals
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Vol. 15 FEBRUARY, 1928 No. 1

A NEW GENUS OF THE ACANTHACEAE[1]

CLARENCE EMMEREN KOBUSKI

Assistant, Arnold Arboretum of Harvard University
Formerly Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

A critical study of herbarium material of the genus *Dyschoriste* has revealed a small group of plants which possess sufficient morphological characters differing from *Dyschoriste* to merit generic recognition.

Apassalus[2] nov. gen. of the Acanthaceae. Calyx profunde 5-fidus. Corolla infundibuliforma; limbus subbilabiatus vel subaequalis; lobi rotundi, convoluti. Stamina 4, didynama, per paria lateraliter contigua vel connata decurrentia; antherae biloculares, basi obtusae, non acutae. Stigmatis lobus anticus obliquus vel dilatus, posticus subnullus. Capsula oblongo-linearis. Semina 2–4, plane compressa, suborbicularia.—Herbae perennes. Foliae ovatae, parvae. Flores parvae, solitarii vel in axillis fasciculati.

Type species: *Apassalus diffusus* (Nees) Kobuski.

Key to Species

A. Capsule 2-seeded; plants covered with short, hirsute, spreading hairs; (Haiti) . . . . . . *A. diffusus*
AA. Capsule 4-seeded; plants glabrous.
  B. Leaves 9–12 mm. long, ovate-subrotund; flowers 8–9 mm. long; (Cuba) . . . . . . *A. cubensis*
  BB. Leaves 25–45 mm. long, ovate-elliptic; flowers 11–12 mm. long; (Am. bor.) . . . . . . *A. humistratus*

A. diffusus (Nees) Kobuski, n. comb. Pl. 1, 2.
Dyschoriste diffusa (Nees) Urb. Symb. Ant. **7**: 380. 1912.

[1] Issued April 30, 1928.

[2] Name dervied from the Greek α, *without* and πάσσαλος, *peg*, on account of the absence of anther appendages.

Dipteracanthus diffusus Nees in DC. Prodr. **11**: 124. 1847.

Dyschoriste humistrata Lindau in Urb. Symb. Ant. **2**: 188. 1900, not O. Ktze., namely, as to plants of Santo Domingo.

Stems somewhat tetragonal, slender, shortly hirsute, ascending from a perennial base, nodes closely placed, 1–2.5 cm. distant; leaves suborbicular-obovate, broadly obtuse at the apex, narrowing into a petiolate cuneate base, shortly hirsute on both surfaces, entire, 10–13 mm. long, 5–9 mm. wide; inflorescence bracteate, axillary; calyx 6–7 mm. long, lobes linear-acuminate, ciliate, ⅔ total length; corolla white (ex Buch) or pale lilac (ex Tuerckheim), puberulent on the external surface, 7–8 mm. long, tube extending into a slightly ampliated throat, lobes rounded; anthers didynamous, filaments slightly pilose at the base, anther cells parallel or nearly so, truncate or rounded at the base; ovary 2-celled, glabrous, style linear, pubescent a little above the base, stigma dilated, oblique; capsule 6–7 mm. long, 2-celled, each cell containing a single seed attached by the retinaculum, both of which (retinacula) are situated on the central ridge of the commissural surfaces; seeds flat, orbicular, becoming mucilaginous when wetted.

Distribution: Islands of Haiti and Santo Domingo.

Specimens examined:

Haiti: on rocky outcrop, dry wooded mountain slope, vicinity of St. Marc, 25–28 Feb. 1920, *E. C. Leonard 2913* (US, G); dry bank along road near Ennery, Dept. of Artibonite, 325–900 m. alt., 13 Jan. 1926, *E. C. Leonard 8823* (US); arid thickets, northeast of the N. West Indies Company, vicinity of St. Michel de l'Atalaye, Dept. du Nord, 300 m. alt., 17 Nov. 1925, *E. C. Leonard 7093* (US); common in dry thickets, vicinity of St. Michel de l'Atalaye, Dept. du Nord, 350 m. alt., 26 Nov. 1925, *E. C. Leonard 7472* (US); Barahona, 1200 m. alt., Sept. 1911, *Fuertes 1407b* (FM, G, US).

Santo Domingo: Azua, March, 1913, *Rose, Fitch & Russel 4072* (US).

A. cubensis (Urb.) Kobuski, n. comb. Pl. 1, 2.

Dyschoriste cubensis Urb. Symb. Ant. **7**: 381. 1911.

Dyschoriste humistrata Lindau in Urb. Symb. Ant. **2**: 188. 1900, not O. Ktze., namely, as to plants of Cuba.

Ruellia diffusa Grisebach, Cat. Pl. Cub. 195. 1866 (excl. syn.); Sauv. Fl. Cub. 97 (no. 1500). 1873.

Low-growing perennial, decumbent, occasionally rising erect, glabrous or minutely scabrous, young stems densely covered with cystoliths; leaves shortly petiolate, ovate to suborbicular, 9–12 mm. long, 5–7 mm. wide, rotund at the apex, tapering to a cuneate base, entire, densely covered with cystoliths on both surfaces, glabrous; flowers solitary, rarely in twos, bracts narrowly obovate; calyx 5-cleft, 6–8 mm. long, lobes linear-acuminate, nearly ⅔ total length, entire external surface covered with cystoliths, glabrous, lobes ciliated; corolla 8–9 mm. long, tube cylindrical, enlarging until ampliated throat is reached, lobes shortly obovate; stamens didynamous, adnate to the middle of the tube, anthers narrowly ovate, obtuse at the base; ovary 2-celled, style linear, nearly glabrous; capsule oblong-linear, 7–8 mm. long, glabrous, 4-seeded; seeds suborbicular, mucilaginous when wetted.

Distribution: near Cojimar, Prov. of Havana, Cuba.

Specimens examined:

Cuba: near Cojimar, Prov. of Havana, 14 March, 1906, *Baker 2894* (FM); shady places in coastal sand between Rio Cojimar and Playa de Bacuranao, Prov. of Havana, 26 Dec. 1910, *Wilson 9533* (G, US).

A. humistratus (Michx.) Kobuski, n. comb. Pl. 1

Dyschoriste humistrata (Michx.) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891.

Ruellia humistrata Michx. Fl. Bor.-Am. **2**: 23. 1803; Pursh, Fl. Am. Sept. **2**: 421. 1814.

Calophanes humistrata Shuttleworth ex. Nees in DC. Prodr. **11**: 108. 1847; Gray, Syn. Fl. N. Am. ed. 1, **2**[1]: 324. 1878, and ed. 2. 1886; Chapman, Fl. Southeastern U.S. ed. 1, 1083. 1860, and ed. 2. 1889.

Dipteracanthus humistratus Chapman, Fl. Southeastern U.S. ed. 2, 303. 1889.

Dipteracanthus riparius Chapman, Fl. Southeastern U.S. ed. 2, 303. 1889.

Stems several, ascending or rising erect from a ligneous perennial base, 4 dm. or less high, glabrous or slightly pubescent;

leaves ovate-elliptic to oblong-sublanceolate, 2.5–4.5 cm. long, 1–2 cm. broad, obtuse to acute at the apex, abruptly attenuated at the base into a petiole which may be so short as to give the leaf a subsessile appearance or as much as 4 mm. long, glabrous or nearly so, entire or slightly crenulate margins; bracts oblong-oblanceolate, about equalling the length of the flower; flowers axillary; calyx deeply 5-parted, 9–10 mm. long, glabrous or slightly pubescent, lobes subulate-setaceous; corolla small, white, 10–11 mm. long, tube 2.5–4 mm. long; stamens didynamous (very seldom 5), filaments pubescent at point of adnation to corolla throat, anther cells obtuse or slightly mucronulate at the base; mature capsule 9–10 mm. long, glabrous, linear, 4-seeded.

Distribution: low grounds, southeastern United States.

Specimens examined:

Georgia: Lumber City on the Ocmulgee River, Telfair Co., July, 1900, *C. Mohr* (US, 721392); shaded places in Ogeechee River swamp, Burke Co., 5 June, 1901, *R. M. Harper 769* (M, US).

Florida: fertile ground under oaks, upper St. John's River, 1 June, *A. H. Curtiss 23* (G); Hot Springs, 7 April, 1925, *H. O'Neill 601* (US); Pine Island, St. John's River, 11 April, 1911, *S. C. Hood* (G); swampy shore of St. John's River, June, 1878, *A. H. Curtiss 1939* (M, FM, G, US); wooded banks of the Suwannee River at Branford, Suwannee Co., 9 June, 1900, *A. H. Curtiss 6654*, (G, M); Suwannee Co., June–July, 1898, *A. S. Hitchcock 1457, 1458* (FM); damp shady places, banks of Rice Creek, Putnam Co., 26 March, 1882, *C. Mohr* (US 721391); Dunnellon, Marion Co., 25 Feb. 1891, *L. F. & R. Ward* (US, 147428); Port Orange, Volusia Co., 20 May, 1895, *F. C. Straub 164* (G); Lake Alfred, Polk Co., 11 June, 1922, *G. M. & J. K. Armstrong* (M 911680); swamp, Hernando Co., June–July, 1898, *A. S. Hitchcock* (M 120820).

Explanation of Plate

PLATE 1

Apassalus diffusus (Nees) Kobuski

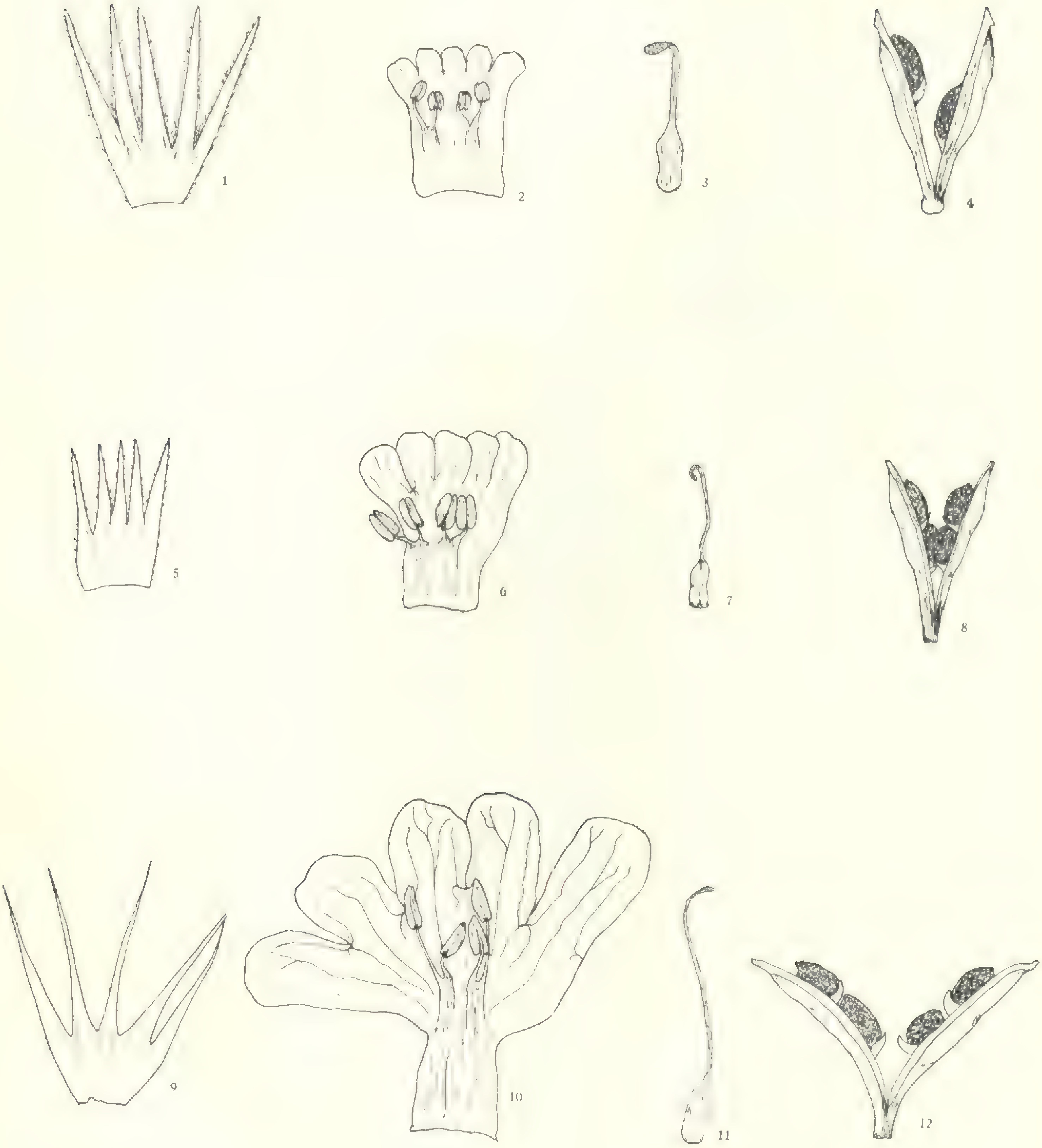
Fig. 1. Open calyx.
Fig. 2. Open corolla showing stamens.
Fig. 3. Pistil.
Fig. 4. Dehiscing capsule showing seeds and retinacula.

Apassalus cubensis (Urban) Kobuski

Fig. 5. Open calyx.
Fig. 6. Open corolla showing stamens.
Fig. 7. Pistil.
Fig. 8. Dehiscing capsule showing seeds and retinacula.

Apassalus humistratus (Michx.) Kobuski

Fig. 9. Open calyx.
Fig. 10. Open corolla showing stamens.
Fig. 11. Pistil.
Fig. 12. Dehiscing capsule showing seeds and retinacula.



KOBUSKI—A NEW GENUS OF ACANTHACEAE

Explanation of Plate

PLATE 2

Fig. 1. *Apassalus diffusus* (Nees) Kobuski

From the specimen, *Fuertes 1407b*, in the United States National Herbarium,

Fig. 2. *Apassalus cubensis* (Urban) Kobuski

From the specimen *Baker 2894*, in the Herbarium of the Field Museum.

KOBUSKI—A NEW GENUS OF ACANTHACEAE

A MONOGRAPH OF THE AMERICAN SPECIES OF THE GENUS DYSCHORISTE[1]

CLARENCE EMMEREN KOBUSKI

Assistant, Arnold Arboretum of Harvard University
Formerly Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

Introduction

Any attempt to determine specifically herbarium specimens of the genus under present consideration formerly proved very unsatisfactory because of the inadequacy of many of the original descriptions and also because of the small representation of type or authentic material in American herbaria. These facts, along with an especial interest in the genus and its allies, led to the present study. At first it was hoped that a monographic treatment of the whole genus might be made. A general survey of the material deposited in American herbaria, however, showed the Old World species to be so poorly represented that it was deemed advisable to exclude them from the present discussion and to include only the American species. Later the writer plans to visit some of the larger European herbaria and to supplement this monograph by a critical study of the far-eastern species.

This investigation was made possible only through the coöperation of the botanists connected with the various herbaria from which material was borrowed. Sincere appreciation is due Dr. B. L. Robinson of the Gray Herbarium, W. R. Maxon of the United States National Herbarium, and D. C. Davies, Director of the Field Museum, who so willingly loaned their entire collections of *Dyschoriste* for this study. It was found necessary also to borrow types, and to obtain fragments and photographs of type collections from several European herbaria. Dr. Santiago Ramón y Cajal, Instituto Cajal, Madrid, and Professor Eduardo Balguerias y Quesada, Jardin Botanico, Universidad de Madrid,

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

Issued April 30, 1928.

very kindly furnished an excellent photograph of a little-known species, the type of which is preserved in the Madrid Herbarium. Professor Boris Fedtschenko, Jardin Botanique Principal, Leningrad, U.S.S.R., obligingly supplied two types essential for the completion of this monograph. Dr. A. W. Hill and T. A. Sprague, Royal Botanic Gardens, Kew, Dr. L. Diels, Botanischer Garten und Museum zu Berlin-Dahlem, Dr. C. H. Ostenfeld and Dr. Carl Christensen, Botanisk Garten, Københavns Universitet, as well as Dr. Adele Lewis Grant, Huguenot College, South Africa, who so willingly made critical comparisons with types at the Kew Herbarium on her journey to Africa, have all contributed either directly or indirectly, in material loaned or in verification of specimens submitted for comparison. The writer takes this opportunity to express his gratitude for their generosity and kindly assistance.

This study was made at the Missouri Botanical Garden, and thanks are due to the Director, Dr. George T. Moore, for the use of the excellent library and herbarium facilities which this institution affords. Also, especial thanks are extended to the Curator of the Herbarium, Dr. Jesse M. Greenman, under whose constant guidance and supervision this work has been made possible.

History

The genus *Dyschoriste* was proposed by Nees in the third volume of Wallich's 'Plantae Asiaticae Rariores' [1] published in 1832. The genus was segregated from *Ruellia* on account of stamen, corolla, and fruit characters, and was based on *Ruellia depressa* Wallich, namely, Wallich's No. 2379 from East India, which, however, is not conspecific with *Ruellia depressa* L. Two other East Indian species, *D. cernua* and *D. litoralis*, were referred by Nees in the same work to his new genus.

In 1833, only a year later, David Don in Sweet's 'British Flower Garden' [2] described the genus *Calophanes*. Don's new genus was also a segregate from *Ruellia*, and was founded on *Ruellia oblongifolia* Michaux, which in turn was based on specimens collected in the state of Georgia.

[1] Wallich, N. Pl. As. Rar. 3: 81. 1832.

[2] Sweet, R. Brit. Fl. Gard. II, 2: 181, *pl. 181*. 1833.

These two generic names were current in botanical literature for many years, as representing two supposedly distinct genera indigenous to remote regions—*Dyschoriste* of the eastern hemisphere and *Calophanes* of the western hemisphere. Nees, the foremost student in his time of the Acanthaceae, in his treatment of this family for Martius' 'Flora Brasiliensis,' [1] in 1847, accepted *Calophanes* and described seven Brazilian species of this genus. The same author and in the same year elaborated the Acanthaceae for DeCandolle's 'Prodromus' [2] and maintained both names as representing separate and distinct genera. In this work, which was the first to present a comprehensive treatment of the group, five species of *Dyschoriste* and twenty-seven species of *Calophanes,* as well as several varieties, were recognized.

Bentham and Hooker in the 'Genera Plantarum,' [3] 1876, treated these two previously supposed distinct generic elements as congeneric, but unfortunately they took up the later name *Calophanes* and relegated *Dyschoriste* to synonymy.

Mr. C. B. Clarke, who contributed the treatment of the Acanthaceae for Hooker's 'Flora of British India,' [4] 1885, followed Bentham and Hooker's generic interpretation of the group and recognized four East Indian species of *Calophanes,* namely, *C. Nagchana* Nees, *C. littoralis* T. Anders., *C. vagans* Wight, and *C. Dalzellii* T. Anders. Under *C. Nagchana* Nees the following species are cited as synonyms: *C. depressa* T. Anders., *Ruellia Nagchana* Ham., *R. erecta* Burm., *R. depressa* and *R. cernua* Nees, *Dipteracanthus Nagchana* Nees, *Dyschoriste depressa,* and *D. cernua* Nees.

In 1891, Dr. O. Kuntze[5] revived the name *Dyschoriste* Nees and transferred thereto several species, including *Ruellia erecta* Burm. which was described and illustrated in 1768, being the oldest known species of this group. Lindau, in 1895, in reviewing the Acanthaceae for Engler and Prantl's 'Die Natürlichen Pflanzenfamilien,' [6] followed Kuntze in recognizing the genus *Dyschoriste.*

[1] Martius, C. F. P. de. Fl. Bras. **9**: 26. 1847.
[2] DeCandolle, A. P. Prodr. **11**: 106, 107. 1847.
[3] Bentham, G. & Hooker, J. D. Gen. Pl. **2**: 1077. 1876.
[4] Hooker, J. D. Fl. Brit. India **4**: 410. 1885.
[5] Kuntze, O. Rev. Gen. Pl. **2**: 486. 1891.
[6] Engler, A. & Prantl, K. Nat. Pflanzenfam. $\mathbf{4}^{3b}$: 302. 1895.

Clarke, in working up the Acanthaceae for the 'Flora Capensis,'[1] 1901, took up the name *Dyschoriste*, thus reversing the position taken by him in Hooker's 'Flora of British India,' mentioned above. He recognized *D. depressa* Nees as a valid species along with four other African species, one of which is *D. erecta* Clarke, thus apparently disregarding the *D. erecta* (Burm.) O. Ktze.

Several new species have been described from time to time and referred to either *Dyschoriste* or *Calophanes*, but no comprehensive treatment of the group as a whole has been published since that of Nees in DeCandolle's 'Prodromus.'

Assuming that there is absolute identity and thus complete synonymy of the several elements which Clarke referred to *Calophanes Nagchana* in the 'Flora of British India,' then, as pointed out by Dr. Kuntze, the name *erecta*, as the oldest specific name involved, must be retained and the binomial *Dyschoriste erecta* (Burm.) O. Ktze. becomes the valid combination for the plant concerned and *D. depressa* (Wall.) Nees must be regarded as a synonym of it. Since this study has been confined to the American species we must admit the observations of Clarke and Kuntze and accept *Dyschoriste erecta* (Burm.) O. Ktze. as the type species of the genus until the eastern species in question can be examined.

General Morphology

Roots.—The root system in the genus *Dyschoriste* is not very extensive. All the species are perennial and the roots, in turn, are of the simple fibrous form. By the casual observer, however, some of the slender underground stems of the previous year's growth are sometimes mistaken for roots.

Stems.—There is considerable variation in the stem and its habit of growth. In all cases, the stem or stems arise from a ligneous perennial base. However, the mode of ascent varies. Many species are prostrate and the stems spread over the ground in several directions. In these cases the leaves assume a secund position. Often when the stems are short a rosette appearance is attained for the whole plant. The species *D. oaxacensis* illus-

[1] Flora Capensis 5^1: 15. 1901.

trates this character. However, it is not a stable specific characteristic. A second habit of growth is the ascending type. It is in this category that the majority of species is placed. The stem not infrequently becomes more or less geniculate; this mode of growth is very characteristic of *D. Pringlei*. The third habit of growth is the erect type. It is to this type that the sturdy *D. hirsutissima*, *D. oblongifolia*, *D. ovata*, and *D. trichanthera* belong. Some species may follow consistently a distinct habit of growth, while others may have the stems ascending or erect even on the same plant. One can usually associate stem growth exceeding a length of 4–5.5 dm. with the erect habit, and shorter stems with the ascending or prostrate habit. Along with this, the prostrate type will possess small leaves and the erect type will have leaves with a more extensive surface.

Several species, among them *D. oblongifolia*, possess slender underground stems which are common in perennials. These stems have the appearance of roots but on close observation buds and modified leaves can be seen. After passing under the ground for some distance they come to the surface and then rise erect.

The stem may be terete or quadrangular. The latter is the more common type in the genus. In the species *D. quadrangularis* the stem is not only angular but the angles are winged. This condition is probably brought about by the decurrent petiole of the leaf extending down the stem.

Leaves.—The leaves of the species in the genus *Dyschoriste* present a great variety of differences. All species have leaves with entire margins, except *D. bilabiata* which is not distinctly dentate but has a decided tendency in that direction. Several species, such as *D. crenulata* and *D. hirsutissima*, show a tendency toward crenulate margins. Others combine the crenulate with the repand margin. Along with these characteristics the margin is usually ciliate. In shape the leaf varies from that of the narrow, linear *D. angusta*, *D. Greenmanii*, and *D. Purpusii* to that of the oblong-ovate *D. quadrangularis* which grows to a length of 10 centimeters. Some species have two types of leaves, the lower or cauline leaves often being larger and different in shape from the upper leaves in whose axils branches and flowers are crowded.

The surface of the leaf itself is usually pubescent. When the pubescence is sparse or absent, an abundance of cystoliths is usually seen. Often the cystoliths, since they lack an orderly arrangement, are mistaken for appressed hairs. This cystolithic character is not sufficiently definite for specific delimitation. Some plants have a more copious formation of cystoliths than others. This character exists on the stem and calyx as well as the leaves. The venation which is very pronounced on the lower surface varies very little within the genus. The usual form is the feather-veined type.

Inflorescence.—In all cases the flowers are axillary and subtended by bracts and sometimes bracteoles. Only occasionally are the flowers solitary in the axils. There are usually several to many flowers at the node, giving the appearance of a cymose cluster as in *D. quadrangularis* or a capitulum as in *D. capitata* and *D. pinetorum*. *D. Greenmanii* is an excellent example of a species with a solitary flower at the node. The majority of species have flowers which are pedicellate, often so short, however, that a subsessile effect is presented.

Calyx.—In the calyx of *Dyschoriste* is found one of the most constant characters of the genus. It is usually five-parted and always persistent. The only deviation from the five-merous condition is found in *D. maranhonis* where the calyx-lobes are occasionally only four. In all cases the lobes are subulate-setaceous and usually ciliate. The ciliation may vary from a long whitish, flaccid pubescence to a very short hirsuteness. When the calyx proper is pubescent, the pubescence is usually confined to the nerves. The tissue connecting the lobes of the calyx is usually very membranaceous and tears apart very easily, making it difficult and quite unsatisfactory to use the ratio between tube-length and lobe-length as a character for specific differentiation. The lobes are usually quite equal in length. However, here again variation is found. Cystoliths, as in the leaves, are very abundant; but in the calyx they are frequently disposed in a more or less regular arrangement.

Corolla.—There is very little differentiation to be found in the corolla of the genus. In most cases the bilabiate type occurs. This, however, is not as distinct as in some other genera of the

Acanthaceae. The corolla is five-lobed, the two posterior lobes being coalescent to a greater extent than the three anterior lobes. The length of the corolla varies from 10 to 17 mm., as found in *D. decumbens, D. hygrophiloides, D. saltuensis, D. quadrangularis,* and *D. angustata,* to 25–28 mm., exemplified in *D. xylopoda, D. humilis,* and *D. ovata.* One species, *D. Pringlei,* has a corolla measuring 35–38 millimeters long. None, however, reach the length of 70–80 millimeters as found in some of the Ruellias. The proportion between tube and throat is variable in the genus. The ventricose throat is found quite often. The condition should exist in all species because of the contiguity of the adnate filaments in the posterior portion of the throat and tube. This ventricosity, hence, is more pronounced in the larger-flowered species. The narrow tube of the corolla is usually slightly flared at the base to make room for the disc and ovary. The ampliation from the tube to the throat is very variable and may be abrupt or gradual according to the species. In all cases, the external surface is quite pubescent. In the species *D. trichanthera* the pubescence is found on the interior as well as the exterior surface of the throat.

Stamens.—The stamens are didynamous. The long and short filaments on each side are contiguous or united at the base by a membrane which extends from the point of adnation to the base of the corolla tube. A very distinctive feature of the anthers is the mucronate appendages at the base of the anther cells. These mucronate appendages are characteristic of the genus and are very easily seen with the hand-lens. Under the low power of the compound microscope they are found to be composed of several multicellular strands of cells closely compacted together. These strands of cells are easily torn apart, and a dentate or ragged appearance is given to the whole appendage. This is doubtless what Nees saw when he described the appendages of *D. quitensis* as "2–3-toothed." A similar example was found in *D. Schiedeana.* On microscopic study, however, the so-called dentations were found to be nothing more than shreds of tissue torn away slightly from the compacted mass. The anther cells are usually parallel and oblong in shape. In the case of *D. sagittata* and *D. maranhonis* the cells are so disposed as to have a

sagittate appearance. In both the species mentioned the apex as well as the base is appendaged. As a rule the anther cells are glabrous but in the species *D. trichanthera* the anther cells are very pubescent. The mode of dehiscence is by a longitudinal slit on the side of the anther cell. The filaments are commonly pubescent.

Pistil.—There is little variation in the parts of the pistil. A disc is present beneath the ovary in all species. The ovary itself is two-celled, glabrous, and oblong. Little or no variation is found in the filiform pubescent style. Only the anterior lobe of the stigma is developed, and this lobe is usually linear and oblique with a flattened stigmatic surface. However, in *D. hygrophiloides* the stigma is curved, while in *D. sagittata* it is basally lobed. In *D. maranhonis* the stigma is reflexed.

Capsule.—The capsule of the genus is quite uniform. The constant linear, glabrous and four-seeded characters, combined with other diagnostic characters, help considerably in generic determination. Retinacula or hooked appendages on the median ridge of the valves hold the flat suborbicular seeds in place. When dry the seeds appear to have many soft, appressed hairs. These same hairs when wetted diverge, elongate, and become mucilaginous.

Geographical Distribution

The geographical distribution of the American species of the genus *Dyschoriste* offers very interesting problems. The accompanying maps demonstrate very clearly that there are three distinct areas of distribution: (1) southeastern United States; (2) southwestern United States and Mexico; and (3) South America.

Two species, namely, *Dyschoriste oblongifolia* and *D. angusta*, occur in the southeastern United States area. This area extends the width of the coastal plain from southern Virginia to southern Florida. The regions of distribution of the two species do not overlap. *D. angusta* is confined to the wet region of Dade and Palm Beach Counties in southern Florida, while *D. oblongifolia* extends northward through the remainder of the area, seeking the dry, sandy pine woods.

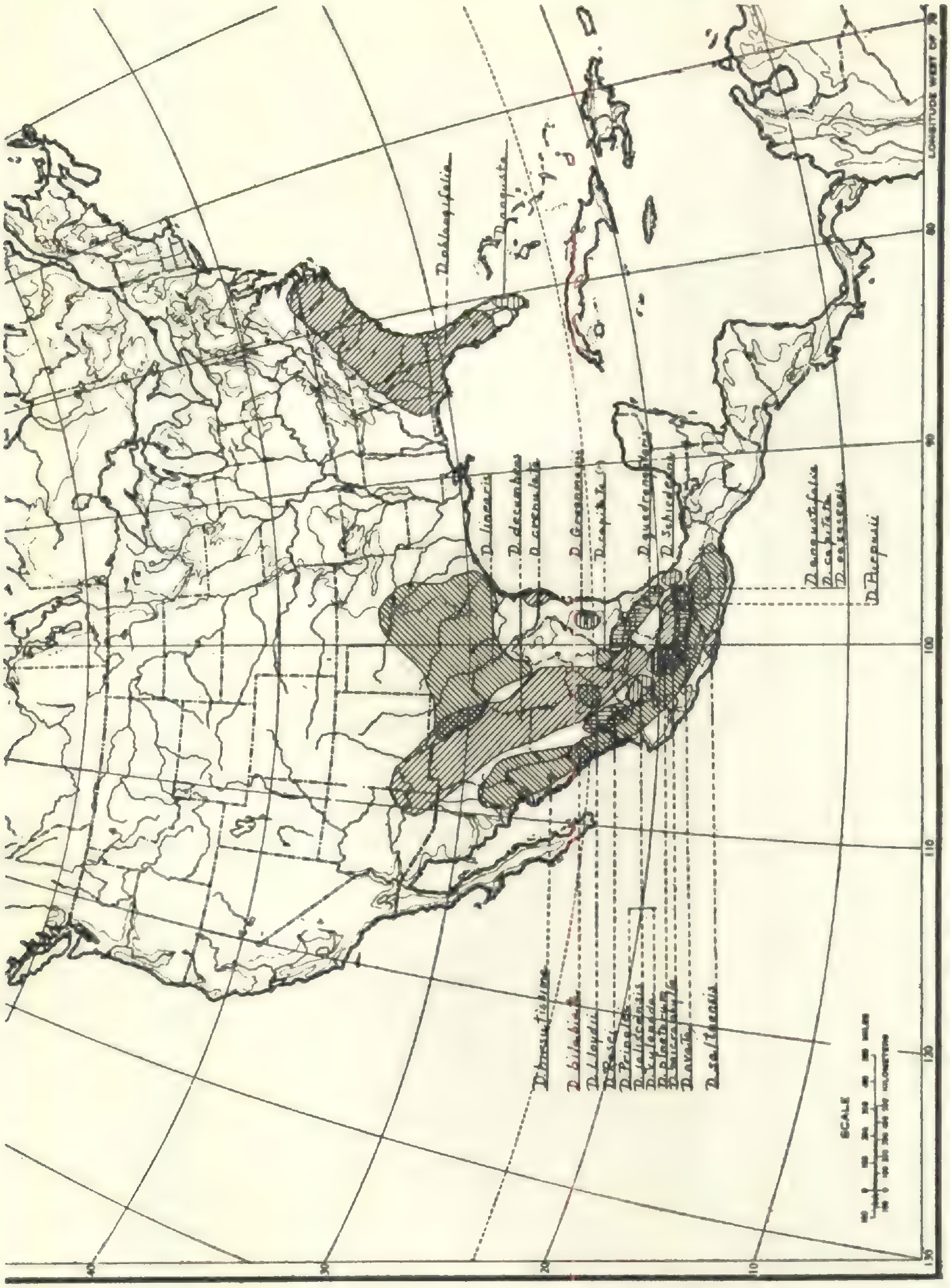


Fig. 1. Map showing the geographical distribution of the North American species of *Dyschoriste.*

The second area extends from Texas and southern Arizona southward to the Isthmus of Tehuantepec and contains the greater number of species. Of the forty recognized species in the genus *Dyschoriste,* twenty-one, or more than half, are confined

Fig. 2. Map showing the geographical distribution of the South American species of *Dyschoriste*.

to this area. It is an interesting fact that the distribution of some species is almost coincident with the geological formation of the country. *D. decumbens*, which occurs on the plateau

region between the Sierra Madre ranges, is an excellent example of this fact. *D. hirsutissima* extends from Sonora southward along the western slope of the Sierra Madre range to Oaxaca. Many species have a localized distribution only, *D. Greenmanii*, *D. crenulata*, *D. saltuensis*, and *D. angustifolia* being examples. Some of these localized areas are characterized by three or more species. An instance of this is a small region around Guadalajara in the state of Jalisco where four species are represented. Another illustration of limited areal distribution occurs in the northern part of Oaxaca which harbors *D. oaxacensis*, *D. angustifolia*, *D. capitata*, and *D. hirsutissima*. Many species, especially the localized ones, appear to be extremely edaphic since they inhabit only regions near volcanoes. The center of distribution in this second area falls within the region represented by the states of Puebla, Michoacan, and Mexico.

The third and last area, namely that of South America, comprises more territory than either of the areas indicated above and includes the seventeen remaining species of the genus. The material examined in all cases was not very copious, hence an accurate range of geographical distribution of these species could not definitely be ascertained. Nearly all species appear to occur in isolated and limited areas, but the relationship between some of these areas indicates that a greater overlapping of areas would occur were it not for the paucity of herbarium material. Three species, namely, *D. quitensis*, *D. ciliata*, and *D. repens*, are found in Peru and the Andes of Ecuador. *D. Niederleinii* and *D. humilis* are found in Argentina. The other thirteen species inhabit northern Paraguay and southern Brazil, and it is here that the South American center of distribution occurs.

An unusual feature of the geographical distribution is the isolation of the areas defined. At present, there is no one species which connects up any two areas. There seems to be no satisfactory explanation to account for the absence of the genus between the Andes of Ecuador and the Isthmus of Tehuantepec in Mexico. Members of the genus may be found between these two remote regions, but until the entire Andean range has been explored more thoroughly from a botanical standpoint one would hardly venture an explanation of the marked discontinuous distribution which the genus now presents.

The non-occurrence of the genus in the Mississippi Valley is equally surprising. Since the flora of this entire area is comparatively well known, it is hardly possible that the members of the genus would be overlooked if they there existed. The only solution seems to be the possible age of the genus. *Dyschoriste* is probably a pre-glacial genus which, prior to the Oligocene period of the Cenozoic era, extended continuously across the southern United States. However, the Eocene and Oligocene seas encroached upon the United States in the present Mississippi Valley, thereby splitting the distribution areas of the genus into two parts.

Phylogeny

Because of the large number of closely allied species in the genus *Dyschoriste* it is quite necessary that the phylogenetic discussion of the group be made from a purely hypothetical standpoint. The fact that the discussion is confined to the American species alone seconds this consideration, since the eastern species of the genus exceed the American species in number.

On account of the three distinct geographical distribution areas, which have been discussed before, a tree method of illustrating probable phylogenetic sequence proved unsatisfactory; hence the method used in the accompanying chart was devised finally to illustrate the apparent relationship of the species of the western hemisphere. This chart if superimposed on a map of the regions inhabited by the genus would coincide with the specific regional distribution.

It was felt reasonably certain that all species of the genus have evolved from a common ancestor designated in the chart as x. From this ancestor, species and groups of species have evolved. One might ask why, since the species seem to be placed in definite groups, subgenera or sections have not been designated. This question was given much thought and consideration; it was felt finally, however, that on account of the relative uniformity of the essential morphological characters within the genus, except in the case of group II, no adequate basis exists for the designation of subgenera or sections.

It may be observed that all the designated groups with the

exception of group II originated from the common ancestor at approximately the same time. Group II, on account of the muticous character of its anther appendages, the extremely small leaves, the very small flowers, and the fruit characters, has been separated from the genus *Dyschoriste* and raised to the rank of a new genus which is considered as intermediate between the hypothetical type and *Dyschoriste* proper. In this genus, *Apassalus*,[1] containing three species, the species *Apassalus diffusus*

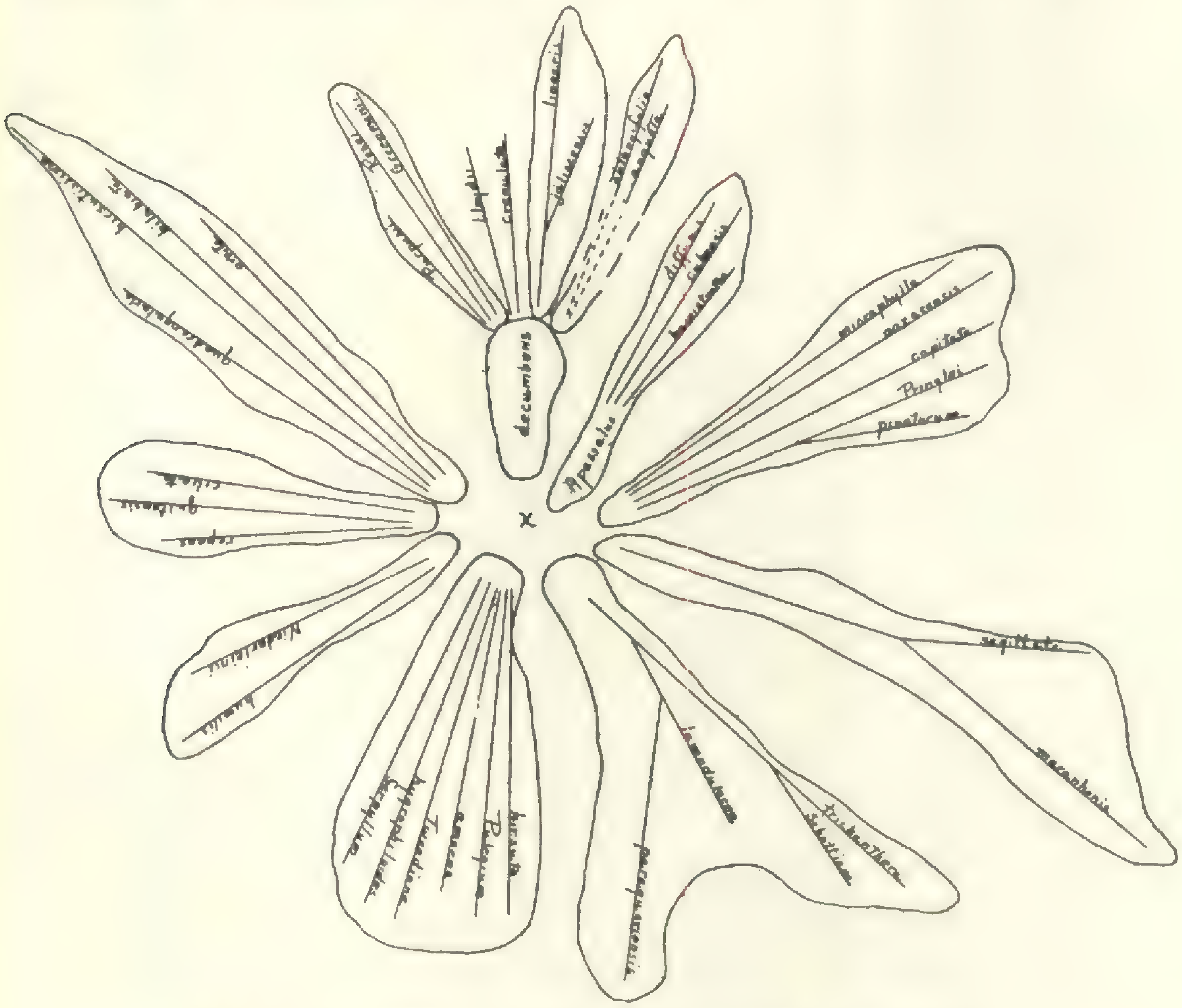


Fig. 3. Phylogenetic chart of the species of *Dyschoriste*.

has reached the highest development in the reduction of the number of ovules to two, one being borne in each valve of the capsule. The other two species contain the four seeds which are characteristic of the majority of species in the genus *Dyschoriste*. *Apassalus* is confined to the islands of Cuba and Haiti and to the southeastern United States.

[1] See Kobuski, C. E. A new genus of the Acanthaceae. Ann. Mo. Bot. Gard. **15**: 1–8, *pl. 1–2*. 1928.

Group I, involving ten species, is confined to the plateau regions of Mexico. In this instance *D. decumbens*, on account of its extended range and characteristic relation to all species concerned, is considered the base species. *D. Lloydii* and *D. crenulata* are species having vital characteristics similar to *D. decumbens* but differing sufficiently in minor characters to be considered direct descendants from the base species. A small group containing three species, *D. Purpusii*, *D. Greenmanii*, and *D. Rosei*, stands by itself. The highest development is reached in *D. Greenmanii* and *D. Rosei* in which cases the inflorescence has been reduced to a solitary flower at each node. All species of the last group have very slender linear leaves.

Another branch from *D. decumbens*, as the chart illustrates, is the *linearis-jaliscensis* branch. Although separated somewhat in regional distribution these two species are closely allied through their flower and foliage structures and are undoubtedly derived from *D. decumbens*.

The species *D. oblongifolia* and *D. angusta* seem to be closely related to *D. linearis;* in fact, *D. linearis* was once considered a variety of *D. oblongifolia*. However, the two species under discussion are confined to the southeastern United States in their distribution and, as the distribution map of North America shows, are not connected definitely with the Mexican-southwestern United States species. This suggests the probability that there may be a relationship between the two species in Florida and the genus *Apassalus* also found there and in the West Indies. The migration may have been northward through the Antilles, and a connecting link between the southeastern United States species and the southwestern United States-Mexico group may never have existed.

In group III, one finds an entirely different situation. Here we have four large, erect species, each showing a definite characteristic development toward advancement. Perhaps the highest development is found in *D. hirsutissima* which extends the length of the western Sierra Madre range and possesses a well-developed glandular pubescence. This is the only instance of this character in the whole genus. *D. bilabiata* and *D. quadrangularis* are close relatives but do not seem to have been derived from the *D. hir-*

sutissima line. Instead, they undoubtedly arose along parallel lines of development. In *D. bilabiata* we find a distinct dentation of the leaf. This group is also characterized by large, petiolate leaves, in some cases as long as ten centimeters, an unusual feature in the genus.

Group IV for the most part occurs in southwest Mexico, that is, the states of Oaxaca, Jalisco, and Michoacan. These species are the ascending foliose type with rather small, ovate leaves. The inflorescence is usually subcapitate, and it is sometimes difficult to distinguish off-hand the species here included. They all, with the exception of *D. pinetorum*, seem to have evolved along a parallel line of development. *D. pinetorum*, on account of its resemblance to *D. Pringlei*, undoubtedly evolved from it. It is in *D. Pringlei* that we find the largest flower of the genus *Dyschoriste*, and in this species a close resemblance is shown to the genus *Ruellia*. The highest point of development in the North American species just discussed is found, according to my opinion, in *D. hirsutissima*, *D. Greenmanii*, *D. Rosei*, and *D. linearis*.

In the South American species of the genus, a similar situation is found. Here the species can be placed in five groups. Group V contains the three species on the western coast inhabiting Peru and Ecuador. Specialization in them is not particularly noticeable. The species *D. ciliata* possesses rather muticous anther appendages. This would ally the species to the genus *Apassalus*. It was necessary to accept the word of Nees in this instance, however, as only a photograph of the type of the species could be obtained.

The species of Group VI are found in Argentina. Here *D. humilis* reaches the highest point of development in the reduced number of seeds. As in *Apassalus diffusus*, only two seeds are produced, a single seed occurring in each valve of the capsule.

Group VII is not unusual in its development. In this group are found six closely related species—perhaps interrelated—but showing no special development. Here again the herbarium material at hand is very sparse, the study in a few instances being confined to photographs.

In Group VIII are four species, two of which are described for

the first time. In the species *D. trichanthera* is found the spicate inflorescence along with pubescent anthers. The former character links it up with *D. Schottiana*, while the latter character shows the relationship which exists between *D. trichanthera* and *D. lavandulacea*. *D. paraguariensis* is undoubtedly a branch from *D. lavandulacea* but possesses more highly developed floral characters.

The last group, namely, group IX, includes only two species. It is here that the sagittate or divergent anther cells are found. The highest development of the group and probably the highest development in the genus is shown by *D. maranhonis*, in which both incomplete didynamy and reduction in corolla and calyx-lobes are found. Nees describes *D. maranhonis* as being glandular-pubescent. A fragment of the type specimen was obtained and failed to demonstrate this character.

Summary

The conclusions drawn as to the probable phylogeny of the group under consideration are reached after a comparative study of the outstanding morphological characters which may be summarized as follows:

(1) Muticous appendaged anthers are more primitive than those with apiculate appendages.

(2) Divergent anther cells are more advanced than parallel anther cells.

(3) Glabrous anthers are more primitive than pubescent anthers.

(4) Four-seeded capsules are more primitive than two-seeded capsules.

(5) Numerous flowers in an axil is a more primitive condition than the solitary-flowered axil because the presence of bracts in the solitary-flowered species shows reduction to have taken place in the telescoping of the inflorescence.

(6) An unlobed stigma is more advanced than the lobed stigma.

(7) Entire-margined leaves are primitive. The dentate margin is an advancement, and the crenulate margin type is intermediate.

(8) Glandulosity is more advanced than pilosity.

(9) Procumbent plants are more primitive than erect plants which have evolved through ascending plants.

(10) Complete didynamy is more primitive than incomplete didynamy.

(11) Winged stems are more advanced than the unwinged quadrangular stems.

(12) Reduction of corolla- and calyx-lobes from five to four is a criterion of specialization and advancement.

Abbreviations

The abbreviations used to indicate the herbaria in which the specimens cited in the present paper occur are as follows:

B = Botanischer Garten und Botanisches Museum, Berlin, Germany.
C = Botanisk Garten, Københavns Universitet, Copenhagen, Denmark.
Ch = University of Chicago (deposited in the Field Museum).
FM = Field Museum of Natural History.
G = Gray Herbarium of Harvard University.
K = Royal Botanic Gardens, Kew, England.
L = Jardin Botanique Principal, Leningrad, U.S.S.R.
M = Missouri Botanical Garden.
Ma = Jardin Botanico, Universidad de Madrid, Madrid, Spain.
US = United States National Herbarium.

Taxonomy

Dyschoriste Nees in Wallich, Pl. As. Rar. **3**: 75, 78. 1832; Nees in DeCandolle, Prodr. **11**: 106. 1847; O. Kuntze, Rev. Gen. Pl. **2**: 485. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4**^{3b}: 302. 1895; Gray, Manual, ed. 7, 743. 1908.

Calophanes D. Don in Sweet, Brit. Fl. Gard. **2**: *pl. 181*. 1833; Nees in Mart. Fl. Bras. **9**: 25. 1847; Nees in DC. Prodr. **11**: 107. 1847; Benth. & Hook. Gen. Pl. **2**: 1077. 1873–76; C. B. Clarke in Hooker, Fl. Brit. India **4**: 410. 1885; Gray, Syn. Fl. N. Am. **2**^{1}: 324. 1878, and ed. 2, 1886; Chapman, Fl. Southeastern U.S., ed. 3, 365. 1897; Small, Fl. Southeastern U.S. ed. 1, 1082. 1903, and ed. 2, 1913.

Linostylis Fenzl. in Linnaea **23**: 94. 1850.

Herbaceous, caulescent perennials, prostrate, ascending or erect, glabrous or pubescent. Leaves opposite, sessile or petioled, usually entire. Inflorescence cymose, capitate or spicate, terminal or axillary. Flowers subtended by foliaceous bracts and bracteoles. Calyx deeply 5-lobed, lobes usually subulate-setaceous, ciliate, lineolate. Corolla-tube usually erect, occasionally slightly ampliated at the base; limb spreading, oblique, obscurely or distinctly bilabiate, 5-lobed. Stamens 4, didynamous; filaments of a long and short stem united at the base and adnate to the base of corolla-tube, pubescent; anther 2-celled, cells oblong, sharply mucronate at the base, parallel or slightly divergent, glabrous or occasionally pubescent. Ovary 2-celled, glabrous, ovules 2 or occasionally 1 in each cell; style filiform, pubescent; posterior lobe of stigma rudimentary, anterior lobe oblique, slightly flattened. Capsule included in the persistent calyx, oblong-linear, glabrous, 2–4-seeded, separating with difficulty at maturity into 2 valves, 1–2 seeds to each valve held in position by retinacula. Seeds flattened, suborbicular, mucilaginous when wetted.

Type species: *Dyschoriste erecta* (Burm.) O. Ktze. in Rev. Gen. Pl. **2**: 485. 1891.

KEY TO SPECIES

1. Plants glandular-pubescent .... *1. D. hirsutissima*
   Plants glabrous or pubescent but not glandular 2
2. Inflorescence spicate 3
   Inflorescence not spicate 4
3. Anther cells pubescent; internal surface of corolla-throat pubescent. .... *2. D. trichanthera*
   Anther cells glabrous; internal surface of corolla-throat glabrous. *3. D. Schottiana*
4. Leaves mostly linear 5
   Leaves ovate, other than linear 14
5. Corolla approximately 10 mm. long .... *4. D. angusta*
   Corolla 15 mm. or more long 6
6. Corolla 15–20 mm. long 7
   Corolla 25–30 mm. long 11
7. Leaves 2 mm. or more wide 8
   Leaves 1 mm. or less wide .... *5. D. Purpusii*
8. Anther cells pubescent .... *6. D. lavandulacea*
   Anther cells glabrous 9
9. Stem glabrous, except for distinct pubescence at node; flowers solitary at node .... *7. D. Greenmanii*
   Stem evenly pubescent; flowers usually two or more at node 10

10. Plants low-growing, ascending, 1 dm. or less high; style approximately 6 mm. long; S. Amer. sp. . . . . 8. *D. Niederleinii*
Plants strict, 3–6 dm. high; style approximately 12 mm. long; Mex. sp. . . . . 9. *D. Schiedeana*
11. Flowers characteristically solitary at the node . . . . 10. *D. Rosei*
Flowers not solitary at the node 12
12. Leaves mostly linear, 2 mm. or less wide . . . . 11. *D. jaliscensis*
Leaves linear to linear-lanceolate, more than 3 mm. wide 13
13. Stem villous-hirsute . . . . 12. *D. angustifolia*
Stem hirsute with rigid hairs . . . . 13. *D. linearis*
14. Leaves distinctly dentate . . . . 14. *D. bilabiata*
Leaves not distinctly dentate 15
15. Cinereous-pubescent throughout 16
Not cinereous-pubescent 17
16. Leaf margins entire, not crenulate . . . . 15. *D. decumbens*
Leaf margins distinctly crenulate . . . . 16. *D. crenulata*
17. Inflorescence capitate or subcapitate 18
Inflorescence other than capitate 21
18. Anthers emarginate, elongate at the apex . . . . 17. *D. capitata*
Anthers without an elongation at the apex 19
19. Corolla 35–38 mm. long . . . . 18. *D. Pringlei*
Corolla 20–21 mm. long 20
20. Leaves glabrous, oblanceolate . . . . 19. *D. oaxacensis*
Leaves pubescent, obovate-elliptic . . . . 20. *D. pinetorum*
21. Corolla 15 mm. or less in length 22
Corolla 20 mm. or more in length 33
22. Leaves sessile 23
Leaves petiolate 25
23. Plants with converging anther cells giving a sagittate appearance; stigma lobed . . . . 21. *D. sagittata*
Plants with parallel anther cells; stigma unlobed 24
24. Plants with glabrous leaves; S. Amer. sp. . . . . 22. *D. Serpyllum*
Plants with pubescent leaves; Mex. sp. . . . . 23. *D. Lloydii*
25. Leaves glabrous 26
Leaves pubescent 28
26. Leaves 6–7 cm. long 27
Leaves 1.5–3 cm. long . . . . 24. *D. microphylla*
27. Anthers distinctly calcarate at base; leaves lanceolate; Mexican species. . . . . 25. *D. saltuensis*
Anthers only slightly calcarate at base; leaves ovate-elliptic; S. Amer. species . . . . 26. *D. ciliata*
28. Stems winged; leaves approximately 10 cm. long . . . . 27. *D. quadrangularis*
Stems not winged; leaves 2–4 cm. long 29
29. Calyx-tube glabrous, lobes ciliate with softly hirsute hairs; leaves lanceolate . . . . 28. *D. quitensis*
Calyx tube pubescent, lobes ciliate with stiffish hairs; leaves ovate to rotund 30
30. Anther cells diverging, giving a sagittate appearance; corolla and calyx lobes frequently reduced to 4; incomplete didynamy common. . . . . 29. *D. maranhonis*

Anther cells parallel; corolla and calyx characters constant; complete didynamy 31
31. Style approximately 5 mm. long 32
Style 10 mm. or more long . . . . . *30. D. hirsuta*
32. Lower leaves obovate to subrotund, emarginate at the apex . . . . . *31. D. hygrophiloides*
Lower leaves ovate, obtuse but not emarginate at the apex . . . . . *32. D. repens*
33. Calyx 9–10 mm. long . . . . . *33. D. Pulegium*
Calyx 15 mm. or more long 34
34. Flowers crowded in glomerules 35
Flowers usually in pairs at the nodes 36
35. Stem erect; corolla barely exceeding or equalling the calyx in length; Mex. sp. . . . . . *34. D. ovata*
Stem geniculate-ascending; corolla 5 mm. or more longer than calyx; S. Amer. sp. . . . . . *35. D. amoena*
36. Leaves pubescent 37
Leaves glabrous 39
37. Villous-pubescent throughout . . . . . *36. D. xylopoda*
Plants not villous-pubescent 38
38. Capsule 4-seeded; N. Amer. sp. . . . . . *37. D. oblongifolia*
Capsule 2-seeded; S. Amer. sp. . . . . . *38. D. humilis*
39. Leaves distinctly acuminate; the two bracts at each axil nearly equalling the leaf in all characters . . . . . *39. D. paraguariensis*
Leaves obtuse at apex; bracts foliate but not equalling the leaf in size 40
40. Leaves sessile; corolla 25–28 mm. long; Am. bor. sp. . . . . . *37a. D. oblongifolia* f. *glabra*
Leaves petiolate; corolla 20 mm. long; S. Amer. sp. . . . . . *40. D. Tweediana*

1. Dyschoriste hirsutissima (Nees) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891.

Calophanes hirsutissimus Nees in DC. Prodr. **11:** 109. 1847; Hemsl. in Biol. Cent.-Am. Bot. **2:** 502. 1882.

Calophanes bilobatus Rose in Contr. U.S. Nat. Herb. **1:** 109. 1891.

Stems branching, ascending from a stout perennial base to a height of 10–12 dm., somewhat quadrangular, more or less pubescent with the pubescence, in some cases, restricted to the edges, occasionally glandular at the apex; leaves petioled, ovate to oblong-ovate, 3–8 cm. long, 1.5–3 cm. wide, acute at both ends, margin usually entire or slightly crenulate, sometimes slightly denticulate, pubescent on both surfaces, younger leaves often densely so and glandular; inflorescence axillary, subtended by glandular-pubescent, subulate bracts; calyx 5-lobed, subulate-setaceous, extremely glandular-pubescent, approximately 11 mm.

long, lobes more than one-half the total length of the calyx; corolla subbilabiate, puberulent on the outer surface, occasionally glandular, averaging 14 mm. in length, tube about the same length as the abruptly ampliated throat; stamens adnate to a little below the middle of the corolla-throat; stigma oblique; capsule 4-seeded; seeds oblique.

Distribution: slopes of the Sierra Madre of western and southern Mexico.

Specimens examined:

Southwestern Chihuahua, Aug.–Nov. 1885, *Palmer 235* (G, US); Alamos, 180 miles s.e. from Guaymas, Sonora, alt. 418 m., 26 March–8 April, 1890, *Palmer 402* (G, US); Sierra de los Alamos Mt., 6 miles due south of town of Alamos, Sonora, 14 March, 1910, *Rose, Standley & Russell 12833* (US); dry hillside, Acaponeta, Tepic, 10 April, 1910, *Rose, Standley & Russell 14298* (US); dry rocky slopes near Guadalajara, Jalisco, 11 Dec. 1888, *Pringle 2154* (G); hills near Guadalajara, Jalisco, 15 Nov. 1889, *Pringle 2939* (FM, G); Cuernavaca, Morelos, 15 Nov. 1865, *Bourgeau 1262* (G); Cuicatlan, Oaxaca, alt. 1000 m., 9 Dec. 1895, *Gonzalez 43* (G); Monte Alban, Oaxaca, 1933 m., 23 Nov. 1894, *Pringle 6053* (G, M, US); Monte Alban, Oaxaca, alt. 2833 m., 24 Nov. 1894, *L. C. Smith 323* (G); Monte Alban, near Oaxaca City, Oaxaca, alt. 1900–2000 m., 23 Nov. 1894, *L. C. Smith 729* (M, US); Monte Alban, Oaxaca, 29 Dec. 1895, *Seler 1733* (G); Valle de Oaxaca, Oaxaca, alt. 1650 m., 18 Nov. 1906, *Conzatti 1521* (FM); Tehuantepec, June, 1906, *Gandoger* (M 120892); Hacienda de Guadalupe, date lacking, *Ehrenberg 1223* (B TYPE, M fragment and photograph).

2. Dyschoriste trichanthera[1] n. sp. Pl. 4.

Dyschoriste maranhonis Lindau in Bull. Herb. Boiss. II. 3: 628. 1903, as to *Fiebrig 4856*, *Hassler 5908*, *7780*, not O. Ktze.

Stems stout, branched, erect, 5–6 dm. high, glabrate, pubescent near the apex, basal portion densely covered with cystoliths, swollen at the nodes; leaves oblong-ovate to ovate, younger

[1] **Dyschoriste trichanthera** Kob., sp. nov., caulibus suffruticosis, erectis, 5–6 dm. altis, glabrescentibus, apice pubescentibus, inferiore cystolitherissimo, tumidis ad nodos; foliis oblongo-ovatis vel ovatis, 5–7 cm. longis, 2–3 cm. latis, integerrimis vel crenulatis, petiolis 10–12 mm. longis; floribus axillaribus, aliquot ad singularos nodos, fere prope apicem spicatis; bracteis parvis, foliaceis, ciliatis, pubescentibus, bracteolis acuminatis, 4–7 mm. longis; calyce 13–14 mm. longo, lobis subulatis, setaceis, 8–9

leaves pubescent, older leaves glabrate, 5–7 cm. long not including the petiole, 2–3 cm. wide, entire to crenulate, petiole 10–12 mm. long; flowers axillary, crowded at the nodes near the apex giving a spicate appearance; bracts small, foliaceous, ciliate and pubescent, bracteoles acuminate, 4–7 mm. long; calyx 13–14 mm. long, lobes subulate-setaceous, 8–9 mm. long, often recurved at the tip, ciliate, with 2 kinds of multicellular hairs, both flaccid and delicate; corolla distinctly bilabiate, 10–20 mm. long, rose or violet, lobes obtuse, emarginate, puberulent on external surface, distinctly pubescent on the internal surface; stamens barely included, adnate to about opposite the labiation of the corolla, anthers pubescent, style filiform, 10–20 mm. long, stigma oblique, linear; capsule not seen.

Distribution: along rivers, northern Paraguay.

Specimens examined:

In the region of the river Capivary, Paraguay, date lacking, *Hassler 5908* (G); between the rivers Apa and Aquidaban, Paraguay, Jan. 1908–9, *Fiebrig 4856* (G); in region along the river Apa, Paraguay, Nov. 1901, *Hassler 7780* (G TYPE, M photograph and fragment).

3. Dyschoriste Schottiana (Nees) Kobuski, n. comb.

Hygrophila Schottiana Nees in Mart. Fl. Bras. **9**: 22. 1847; Nees in DC. Prodr. **11**: 87. 1847.

Dyschoriste crinita (Nees) O. Ktze. Rev. Gen. Pl. **2**: 485. 1891; Lindau in Bull. Herb. Boiss. **7**: 575. 1899.

Calophanes crinitus Nees in Mart. Fl. Bras. **9**: 26. 1847; Nees in DC. Prodr. **11**: 107. 1847.

Herbaceous perennial; stem erect, 5–6 dm. high, profusely branched, hirsute; leaves oblong-lanceolate, 4–5 cm. long, 1–1.5 cm. broad, tapering below into a short petiole, entire, glabrous, margin and midrib of under surface scabrous; inflorescence axillary, cymose, many-flowered, subtended by bracts; calyx deeply

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mm. longis, apice saepe recurvatis, ciliatis cum duobus generibus multicellularum capillorum, ambis flaccidis subtilibusque; corolla bilabiata, 10–20 mm. longa, rosea vel violacea, lobis obtusis, emarginatis, extus puberulentis, interiore anterioris lobis faucorum pubescente; staminibus parce inclusis, antheris pubescentibus; stylo 10–20 mm. longo, stigmata obliqua, lineari; capsula ignota.—TYPE collected along the river Apa, Paraguay, Nov. 1901, *E. Hassler 7780* (G).

5-parted, densely hirsute, about 10 mm. long, lobes subulate-setaceous; corolla more or less bilabiate, approximately 18–20 mm. long, pubescent on the external surface; capsule 8–9 mm. long, 4-seeded, glabrous; seeds flattened, suborbicular.

Distribution: southeastern Brazil.

Specimens examined:

Prov. Goyaz, Brazil, Feb. 1841–42, *Gardner 3951* (K TYPE, M photograph).

4. **Dyschoriste angusta** (Gray) Small, Fl. Miami, 168. 1913; Small, Fl. Florida Keys, 135. 1913.

Calophanes angusta Gray, Syn. Fl. N. Am. ed. 2, 2^1: 456. 1886; Small, Fl. Southeastern U.S. ed. 1, 1083. 1903, and ed. 2, 1913.

Calophanes oblongifolia var. *angusta* Gray, Syn. Fl. N. Am. ed. 1, 2^1: 324. 1878, and ed. 2, 1886.

A low-growing perennial, 1–2 dm. high; stem erect or ascending from a creeping base, slightly puberulent, occasionally branching; leaves many, subsessile, linear to linear-lanceolate, 1.5–2 cm. long, lineolate, entire; bracts foliaceous, about one-half as long as the leaves; flowers axillary; calyx 8–9 mm. long, lobes subulate-setaceous, ciliate, distinct to near the base, hardly surpassing the capsule at maturity; corolla blue, purple, or rarely, white, slightly bilabiate, approximately 1 cm. long, tube slightly shorter than the limb and a little ampliated at the base; stamens adnate to the base of the limb of the corolla; anthers ovate, filaments widening at the base; capsule glabrous, linear, 4-seeded; seeds somewhat oblique.

Distribution: southern Florida.

Specimens examined:

Palm Beach County: Palm Beach, 26 Dec. 1895–11 Jan. 1896, *Hitchcock 1455* (FM).

Dade County: pine lands, Grossmanns, 24 May, 1904, *Britton 155* (FM); Cocoanut Grove, 26 Dec. 1895, 11 Jan. 1896, *Hitchcock 1456* (FM); Miami, near river, 21 Nov. 1903, *Eaton 385* (FM); in pine lands between Cocoanut Grove and Cutler, 13–23 Nov. 1903, *Small & Carter 776* (FM); cabbage field in pine woods, Grossmanns, 25 Feb. 1905, *Eaton 1247* (G); Biscayne Bay, 1874, *Palmer 347* (G, M, US); Miami, May, 1877, *Garber* (G, M

120923); Biscayne Bay, June, 1880, *Curtiss 1938* (G); Lemon City, 3 March, 1892, *Simpson 528* (G, US); rocky, calcareous land, Miami, 6 April, 1897, *Curtiss 5858* (M, FM, G, US); Black Point Bridge near Cutler, 27 Feb. 1920, *Young 301* (US).

5. Dyschoriste Purpusii[1] n. sp. Pl. 5.

Perennial, erect or ascending from a suffruticose base, branching quite profusely, more or less pubescent, with short, stout, white hairs; leaves sessile, linear to linear-lanceolate, 18–20 mm. long, 1 mm. or less broad, entire, pubescent; flowers slightly pedicellate, subtended by two foliaceous bracts; calyx 5-parted, 9–11 mm. long, lobes unequal, slightly longer than the tube, pubescent, ciliate; corolla 15–17 mm. long, pubescent on the external surface, tube very narrow, not ampliated at the base, approximately 7 mm. long, limb 4 mm. long; anthers of the shorter pair of stamens occasionally smaller; style 11–12 mm. long, stigma oblique; capsule linear, glabrous, approximately 10 mm. long; seeds 4, oblique.

Distribution: south Mexico.

Specimens examined:

Puebla: rocky hills, Tehuacan, June, 1905, *Purpus 2362* (M TYPE, US, G, FM); vicinity of San Luis Tultitlanapa, July, 1908, *Purpus 3347* in part (M).

6. Dyschoriste lavandulacea (Nees) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891.

Calophanes lavandulaceus Nees in Mart. Fl. Bras. **9**: 27. 1847; Nees in DC. Prodr. **11**: 112. 1847.

Stems erect from a perennial base, 1.5–2 dm. high, sparingly pubescent, quite angular; leaves sessile, linear-lanceolate, 40–50

[1] **Dyschoriste Purpusii** Kob., sp. nov., caulibus perennis, erectis vel ascendentibus a suffruticosa basi, ramis profusis, plus minusve pubescentibus cum brevibus albidis capillibus; foliis sessilibus, linearibus vel linearo-oblanceolatis, 18–20 mm. longis, 1 mm. minusve latis, integerrimis, pubescentibus; floribus parum pedicellatis, subtendentibus bracteis; calyce 5-diviso, 9–11 mm. longo, lobis inaequalibus, paulo tubo longioribus, pubescentibus, ciliatis; corolla extus puberula, 15–17 mm. longa, tubo angustissimo, non ampliato ad basem, plus 7 mm. longo, limbis 4 mm. longis; staminibus postero-lateralibus minoribus; capsula lineari, glabra, 10 mm. longa, 4-sperma.—TYPE collected on rocky hills, Tehuacan, June, 1905, *C. A. Purpus 2362* (M).

mm. long, 4–5 mm. wide, tapering to an acute apex, entire, glabrous; inflorescence somewhat glomerulate, several-flowered; bracts minute, 3–5 mm. long, resembling the calyx in texture; calyx 5-lobed, 13–14 mm. long, tube about 5 mm. long, glabrous and covered with cystoliths except for the ciliate, subulate-setaceous lobes; corolla 5-lobed, slightly bilabiate, 20 mm. long, pubescent on the external surface, tube one-half the total length of the corolla, lobes quite truncate; anther cells slightly puberulent; mature capsule not seen.

Distribution: south-central Brazil.

Specimens examined:

In dry fields, near Rio Pardo, Brazil, Sept. 1826, *Riedel 501* (L TYPE, M photograph).

7. Dyschoriste Greenmanii[1] n. sp. Pl. 6.

Plants about 2 dm. high, ascending from a perennial base; stems slender, branched, pubescent at the nodes, otherwise quite glabrous; leaves sessile, linear, 20–25 mm. long, approximately 2 mm. broad, entire, ciliate, sparingly pubescent; flowers few, solitary at the nodes, subtended by 2-foliaceous bracts; calyx deeply 5-parted, 15 mm. long, flaccid-pubescent on the main nerves; lobes subulate-setaceous, approximately 10 mm. long; corolla pubescent on the external surface, 17 mm. long, scarcely exceeding the calyx in length, tube 6.5–7 mm. long, throat more or less equalling the tube in length; style 12 mm. long, pubescent, stigma oblique; capsule linear, glabrous, 7–8 mm. long, 4-seeded.

Distribution: northeastern Mexico.

Specimens examined:

Vicinity of Victoria, Tamaulipas, alt. 320 m., 1 May–13 June, 1907, *Palmer 492* (US TYPE, M photograph and fragment).

[1] **Dyschoriste Greenmanii** Kob., sp. nov., planta prope 2 dm. alta, ascendens a perenne basi; caulibus gracilibus, ramosis, pubescentibus ad nodos, aliter glabris; foliis linearibus, sessilibus, 20–25 mm. longis, 2 mm. latis, integerrimis, ciliatis, parce pubescentibus; floribus paucis, solitariis ad nodos, subtendentibus 2-foliaceis bracteis; calyce profunde 5-diviso, 15 mm. longo, flaccido-pubescente nervis, lobis subulato-setaceis, prope 10 mm. longis; corolla 17 mm. longa, paulo calyce longiore, tubo 6.5–7 mm. longo, fauce plus minusve aequante tubum; stylo 12 mm. longo, pubescente, stigmata obliqua; capsula lineari, glabra, 7–8 mm. longa, 4-sperma.—TYPE collected in the vicinity of Victoria, Tamaulipas, Mexico, 1 May–13 June, 1907, *E. Palmer 492* (US).

8. Dyschoriste Niederleinii Lindau in Engl. Bot. Jahrb. **19** (Beibl. 48): 15. 1894.

Low-growing perennial; stems ascending, about 1 dm. high, branches tetragonal, minutely puberulent; leaves linear, approximately 30 mm. long, 5 mm. broad, somewhat obtuse at the apex, entire, glabrous, sparsely pilose at the base, petiole 2 mm. long; flowers single, axillary, subtended by small bracts; calyx 5-parted, puberulent, 11 mm. long, tube and calyx lobes of equal length; corolla puberulent on the external surface, 15 mm. long, ventricose; style 6 mm. long, filiform, pubescent; mature capsule unknown.

Distribution: Argentina.

Specimens examined:

"Ad Primer Misionero de Hernandez," *Puck and Fernandez* (*Niederlein 42*), Argentina, Feb. 1884, (B TYPE, M photograph).

9. Dyschoriste Schiedeana (Nees) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891.

Calophanes Schiedeanus Nees in DC. Prodr. **11:** 111. 1847; Mueller in Walpers, Ann. **5:** 647. 1858, including var. *multiflorus;* Hemsl. in Biol. Cent.-Am. Bot. **2:** 502. 1882.

Perennial, ascending or erect from a suffruticose base, 3–6 dm. high; stems somewhat angular, hirsute, branched near the base; leaves usually linear-lanceolate, lower cauline leaves occasionally obovate, 20–25 mm. long, 3–5 mm. broad, acute at the apex, narrowed at the base into a very short petiole, entire, hirsute on both surfaces; flowers axillary, usually two in an axil, subtended by bracts which equal or nearly equal the calyx in length; calyx 5-parted, 11–12 mm. long, lobes 7 mm. long, subulate-setaceous, hirsute; corolla 14–15 mm. long, pubescent on external surface, tube 4 mm. long; mature capsule 7–8 mm. long, linear, glabrous, acute at apex, 4-seeded; seeds typical.

Distribution: eastern Mexico.

Specimens examined:

Nuevo Leon: near Monterey, alt. 550 m., Aug. 1911, *Arsène 6411* (US).

Vera Cruz: in fields near Jalapa, date lacking, *Schiede 122* (M photograph of type, B TYPE); Mirador, date lacking, *Sartorius* (US 55268).

10. Dyschoriste Rosei[1] n. sp. Pl. 7, fig. 1.

Low-growing perennial; stem pubescent, branched, ascending or erect, 12–15 cm. high; leaves sessile, linear, entire, glabrous, 18–25 mm. long, 2 mm. broad; flowers few, solitary at the nodes, usually near the apex of the stem, slightly pedicellate, subtended by 2-foliaceous bracts; calyx 5-parted, glabrous except for the ciliate margin of the unequal, subulate-setaceous lobes, shorter posterior lobes 8–9 mm. long, anterior lobes 11–12 mm. long; corolla externally pubescent, 25 mm. long, tube 10 mm. long, diverging abruptly into a broadly ampliated throat which is approximately equal the tube in length; stamens occasionally incompletely didynamous; ovary 2-celled, each cell containing 2 ovules, style 17–18 mm. long, stigma oblique, 2 mm. long; mature capsule not seen.

Distribution: western Mexico.

Specimens examined:

Durango: without definite locality, 13 Aug. 1897, *Rose 2259* (US TYPE, M fragment and photograph).

Jalisco: on road between Mesquite and Monte Escolebo, 26 Aug. 1897, *Rose 3581* (US).

11. Dyschoriste jaliscensis[2] n. sp. Pl. 8.

Stems several, 3–4 dm. high, erect from a ligneous, perennial base, branching, pubescent; leaves linear to linear-oblanceolate, 2.5–3.5 cm. long, 2 mm. or less broad, narrowed at the base,

[1] **Dyschoriste Rosei** Kob., sp. nov., humilis perennis; caule pubescente, ramis ascendentibus vel erectis, 12–15 cm. altis; foliis linearibus, sessilibus, 18–25 mm. longis, 2 mm. latis, integerrimis, glabris; floribus paucis, solitariis ad nodos, fere prope apicem, subpedicellatis, subtendentibus bracteis; calyce 5-diviso, glabro, lobis inaequalibus, subulato-setaceis, posterioribus lobis 8–9 mm. longis, anterioribus lobis 11–12 mm. longis; corolla extus puberula, 25 mm. longa, tubo 10 mm. longo, divergente subito in late ampliato fauce; staminibus didynamis, subinde imperfectis; ovario biloculo, stylo 17–18 mm. longo; stigma obliqua, 2 mm. longa; capsula ignota. —TYPE collected in the state of Durango, 13 Aug. 1897, *Rose 2259* (US).

[2] **Dyschoriste jaliscensis** Kob., sp. nov., planta 3–4 dm. alta; caulibus pluribus, erectis a lignoso basi, ramis pubescentibus; foliis linearibus, linearo-oblanceolatis, 2.5–3.5 cm. longis, 2 mm. minusve latis, basi attenuatis, integerrimis, pubescentibus; floribus maioribus, bracteis foliaceis, 10 mm. longis; calyce 17–18 mm. longo, pubescente, lobis 11–12 mm. longis, subulato-setaceis, ciliatis; corolla prope 30 mm. longa, tubo 12–13 mm. longo, pauce fauce longiore; antheris 2 mm. longis, basi bicalcaratis; stylo 20–21 mm. longo, stigmata obliqua, capsula ignota.—TYPE collected on rocky hills near Guadalajara, Jalisco, 27 June, 1893, *Pringle 5481* (G).

entire, pubescent; flowers comparatively large, subtended by 2-foliaceous bracts which are about 10 mm. in length; calyx 17–18 mm. long, pubescent, lobes 11–12 mm. long, subulate, setaceous, ciliate; corolla approximately 30 mm. long, tube 12–13 mm. long, slightly longer than the throat; anthers about 2 mm. long; style 20–21 mm. long, stigma oblique; mature capsule not seen.

Distribution: western Mexico.

Specimens examined:

Jalisco: rocky hills near Guadalajara, 27 June, 1893, *Pringle 5481* (US, G TYPE, M photograph and fragment).

12. **Dyschoriste angustifolia** (Hemsl.) O. Ktze. Rev. Gen. Pl. **2**: 485. 1891.

Calophanes angustifolius Hemsl. in Biol. Cent.-Am. Bot. **2**: 502. 1882.

Stem erect, strict, 4–5 dm. tall, more or less villous-hirsute; leaves subsessile, linear-lanceolate, 1.5–2.5 cm. long, 3–5 mm. broad, acute at the apex, attenuate at the base, entire, scabrous; flowers axillary, disposed in dense shortly pedunculate cymes in the axils of the upper leaves, subtended by narrow bracts which almost equal the calyx in length; calyx deeply 5-parted, 15 mm. long, scabrous, lobes subulate-setaceous, nearly equalling the tube of the corolla, ciliate; corolla bilabiate, puberulent on the external surface, approximately 25 mm. long; anther cells shortly mucronate at the base; ovary 2-celled, cells 2-ovulate, glabrous, stigma linear, oblique; mature capsule not seen.

Distribution: southern Mexico.

Specimens examined:

Oaxaca: without definite locality, coll. of 1842, *Ghiesbreght* (K, M photograph).

13. **Dyschoriste linearis** (Torr. & Gray) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4^{3b}**: 302. 1895; Lindau in Bull. Herb. Boiss. II. **6**: 844. 1906.

Dipteracanthus linearis Torr. & Gray, Bost. Jour. Nat. Hist. **5**: 50. 1845 (Pl. Lindh. **1**: 50).

Calophanes linearis Gray, Syn. Fl. N. Am. **2^1**: 324. 1878, and

ed. 2, 1886; Hemsl. in Biol. Cent.-Am. Bot. **2:** 503. 1882; Small, Fl. Southeastern U. S. 1083. 1903, and ed. 2, 1913.

Calophanes oblongifolius var. *texensis* Nees in DC. Prodr. **11:** 108. 1847; Torr. in Emory's Rept. U.S. & Mex. Bound. Surv. **2** (Bot.): 122. 1859.

Calophanes ovatus Nees in DC. Prodr. **11:** 108. 1847, not *Ruellia ovata* Cav.

Ruellia ovata Benth. Pl. Hartweg. 89. 1842, not Cav. i.e., as to plant of Drummond from Texas.

Stem 18–42 cm. high, erect and strict, branched and diffuse, hirsute with both rigid and short hairs, sometimes sparsely pubescent or nearly glabrous, not cinereous; leaves linear-oblanceolate to oblong-spathulate, 1.8–6.5 cm. long, entire, lineolate, rather rigid, pubescent on midrib and veins, margin ciliate; bracts foliaceous, frequently in short-leafed specimens equalling the length of the leaf; calyx 5-cleft, densely lineolate, giving the appearance of appressed hairs, lobes 9–13 mm. long, subulate-setaceous, more or less hispid, ciliate, calyx tube 4.5–6 mm. long, in most cases one-half the length of the lobes; corolla somewhat bilabiate, 26–27 mm. long, pubescent on external surface, tube 5–7 mm. long and slightly shorter than the abruptly ampliated limb; anther cells oblong; capsule 4-seeded; seeds flat.

Distribution: Texas to New Mexico and northern Mexico.

Specimens examined:

Texas: rocky prairies, 12 July, 1903, *Reverchon* (M 120836); western Texas, 1890, *Nealley* (Ch 254803); 1846, *Lindheimer 504* (US); *Drummond 2 no. 178* (G TYPE); *Drummond 256* (G); dry prairies, Bay City, Matagorda Co., 6 May, 1916, *Palmer 9667* (M); prairies, Ganado, Jackson Co., 20 March, 1916, *Curtiss 9216* (M); dry open ground, Vanderbilt, Jackson Co., 10 May, 1916, *Palmer 9708* (M); Calhoun Co., 10 Aug. 1920, *Drushel 4136* (M); dry rocky prairies near Dallas, Dallas Co., June–July, *Curtiss 1941* (FM, M); dry rocky prairies, Dallas, Dallas Co., May–June, 1879, *Reverchon* (FM 88468); dry rocky prairies near Dallas, Dallas Co., date lacking, *Reverchon 1941* (G, M, US); rocky limestone prairies, Dallas Co., 15 May, *Reverchon 722* (M, US); Dallas Co., 23 May, 1903, *Bebb 1343* (FM); rocky prairies, Dallas Co., 18 May, 1900, *Reverchon 2114* (M); field and gardens, Fort Worth,

Tarrant Co., 8 June, 1909, *Ruth 104* (US); along roadsides near Fort Worth, Tarrant Co., 5 July, 1909, *Ruth 30* (FM); dry grounds near Fort Worth, Tarrant Co., 1 June, 1910, *Ruth 81* (FM); Austin, Travis Co., 25 June, 1920, *Tharp 733* (US); Austin, Travis Co., 1897, *Buckley* (M 120803); dry hills, Austin, Travis Co., 13 May, 1872, *Hall 431* (G); dry prairies, Austin, Travis Co., 16 May, 1872, *Hall 428* (US); along Corpus Christi Bay, Nueces Co., alt. sea level, 9–12 April, 1894, *Heller 1529* (G, M US, FM); dry open ground, Strawn, Palo Pinto Co., 27 June, 1918, *Palmer 14252a* (M); Dublin, Erath Co., 1893, *Maxwell 49* (Ch); Round Top Mt., Comanche Co., 9 May, 1900, *Eggert* (M, 120809); Gillespie Co., date lacking, *Jermy 472* (M); rich hillside, Boerne, Kendall Co., 19 May, 1916, *Palmer 9811* (M); in dried river beds of mountain rivers north of Braunfels, Comal Co., 1846, *Lindheimer 325* (M); in pastures, Bracken, Comal Co., 3 Aug. 1903, *Groth 230* (G); humid prairie and along margin of shrubs near New Braunfels, Comal Co., May, 1848, *Lindheimer 677* (G, M, FM, US); in grass and on black prairie loam, New Braunfels, Comal Co., May, 1846, *Lindheimer 111* (G, M); Comanche Springs, New Braunfels, Comal Co., May, 1851, *Lindheimer 1063* (M, G, FM, US); New Braunfels, Comal Co., May, 1851, *Lindheimer 552* (M); in open pastures, 5 miles south of San Antonio, Bexar Co., 14 May, 1920, *Schultz 146* (US); San Antonio, Bexar Co., 1918, *Slater* (US 891769); San Antonio, Bexar Co., 1884, *Havard* (Ch 252081); Bexar Co., date lacking, *Jermy 62* (M, US); San Antonio, date lacking, *Jermy 249* (G); San Antonio, Bexar Co., 27 April, 1911, *Mr. & Mrs. Clemens 1069* (M); Bexar Co., date lacking, *Jermy 31* (US); San Diego, Duval Co., 1885, *Croft 6465* (M); San Diego, Duval Co., July, 1885, *Croft 6660* (M); dry open ground, Baird, Callahan Co., 26 May, 1918, *Palmer 13698* (M); Abilene, Taylor Co., 22 May, 1902, *Tracy 8079* (G, M, FM, US); prairie north of Abilene, Taylor Co., 7 June, 1900, *Eggert* (M 120800); calcareous banks, Menard Co., 11 May, 1917, *Palmer 11871* (M); dry alluvial soil along creek, Lacey's ranch, Kerr Co., 10 June, 1917, *Palmer 12229* (M); rocky ground, Sweetwater, Nolan Co., 27 May, 1918, *Palmer 13758* (M); Knickerbocker ranch, Dove Creek, Tom Green Co., May, 1880, *Tweedy 180* (US); Fort Clark, Kinney Co., 10 May, 1893, *Mearns 1432*

(US); Devils River, Valverde Co., May, 1913, *Orcutt 6230* (M); prairie north of Stanton, Martin Co., 13 June, 1900, *Eggert* (M 120810); western Texas to El Paso, New Mexico, El Paso Co., May–Oct. 1849, *Wright 432* (G, FM, US).

New Mexico: Slaughter Canyon, Guadalupe Mts., 12–20 Aug. 1924, *Standley 40624* (US).

Mexico: Sierra Madre, 45 miles south of Saltilla on border of states of Coahuila and Nuevo Leon, July, 1880, *Palmer 2033* (G); roadside, Piedras Nigras, Coahuila, May, 1883, *Havard* (Ch 267840, US 147426); near Huasemote, Durango, 15 Aug. 1897, *Rose 3495* (US).

14. **Dyschoriste bilabiata** (Seemann) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891; Lindau in Bull. Herb. Boiss. **7**: 575. 1899. Pl. 9.

Calophanes bilabiatus Seem. Voy. H. M. S. Herald, 324. *pl. 65.* 1852–57; Hemsl. in Biol. Cent.-Am. Bot. **2**: 502. 1882.

Stems 6–7 dm. high, erect from a perennial base, branching, pubescent; leaves ovate-oblong, 4–5 cm. long, 1.5–2 cm. broad, acute at the apex, narrowed at the base into a petiole, repand-denticulate, densely pubescent on both surfaces; flowers axillary, cymose, cymes pedunculate, 3–5-flowered, subtended by subulate bracts; calyx 5-lobed, 12 mm. long, tube 5 mm. long, pubescent, lobes subulate-setaceous, ciliate; corolla subbilabiate, pale blue, 14 mm. long, tube 5–6 mm. long, subventricose, pubescent on the external surface; filaments hairy; ovary glabrous, style filiform, stigma linear, oblique; mature capsule linear, glabrous, 4-seeded.

Distribution: western Mexico.

Specimens examined:

Cero de Pinal, Sinaloa, Dec. 1848, *Seemann 1513* (K TYPE, M photograph only).

15. **Dyschoriste decumbens** (Gray) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4**^{3b}: 302. 1895.

Calophanes decumbens Gray, Syn. Fl. N. Am. ed. 1, **2**^{1}: 325. 1878, and ed. 2, 1886; Hemsl. in Biol. Cent.-Am. Bot. **2**: 502. 1882.

Calophanes oblongifolius Torr. Bot. Mex. Bound. Surv. 122. 1855, not Don.

Cinereous-puberulent throughout; stems mostly spreading on the ground from a ligneous base, occasionally erect, branched; leaves spatulate to oblanceolate, 2–3 cm. long, 0.5–1.1 cm. broad, entire, apex usually obtuse, sometimes slightly mucronate, base attenuated, often having the appearance of a petiole; flowers few, in foliose, bracteate clusters; calyx 15–20 mm. long, at maturity exceeding the capsule by as much as 10 mm., 5-cleft, tube 5–7 mm. long, lobes subulate-setaceous, hardly twice the length of the tube; corolla purple, 18–20 mm. long, tube a little longer than the throat, slightly ampliated at the base; anther cells oblong, filaments united at the base of the corolla-throat; seeds 4, suborbicular and flattened.

Distribution: dry soil, western Texas to Arizona, and the plateau region of northern Mexico.

Specimens examined:

Texas: Chenates region of western Texas, 1889, *Nealley 580* (*357*) (US); infrequent on slopes between Marfa and Alpine, 15 April, 1919, *Hanson 638* (US).

New Mexico: Valley of the Rio Grande, 1851, *Wright 1462*, *1463* (M).

Arizona: Sonoito Valley, Santa Cruz Co., alt. 1833 m., Aug. 1874, *Rothrock 637* (US); Fort Huachuca, 1890, *Patzky* (US 721394); Fort Huachuca, Cochise Co., May, 1892, *Wilcox* (US 55273, M 120796); roadway, Chiricahua Mts., Cochise Co., alt. 1400 m., 9 Oct. 1907, *Blumer 2223* (FM); Fort Huachuca, Cochise Co., 1894, *Wilcox 150* (US); foothills of Santa Rita Mts., near Greaterville, Pima Co., alt. 1666 m., 16 Sept. 1916, *Shreve 4978* (US); plains about Huachuca Mts., Aug. 1882, *Lemmon* (US 55278); locality lacking, 1875, *Rothrock* (US 55277); Fort Huachuca, Cochise Co., 26 April–21 May, 1890, *Palmer 472* (US).

Mexico: Sierra Mojado Mts., Coahuila, 19 April, 1892, *Jones 374* (US, M); near the border of Coahuila and Nuevo Leon, Feb.–Oct. 1880, *Palmer 1009* (US); Saltillo, Coahuila, alt. 1600 m., 1911, *Arsène 6472* (US); Saltillo, Coahuila, July, 1880, *Palmer 2032* (G); Saltillo, Coahuila, May, 1898, *Palmer 125* (US, M); Lerios, 15 leagues east of Saltillo near the border of Coahuila and

Nuevo Leon, alt. 3000 m., 10–13 July, 1880, *Palmer 1010* (*15453*) (US, M); on road near Colatlan, Zacatecas, 31 Aug. 1897, *Rose 3615* (US); exact locality lacking, San Luis Potosi, 1897, *Schaffner 354* (*647*) (US); San Luis Potosi, alt. 2000–2500 m., 1878, *Parry & Palmer 699* (FM, M, G, US); near Queretaro, 20–23 Aug. 1909, *Rose & Rose 11148* (US); San Andres Mts., Chihuahua, 22 Aug. 1900, *Trelease 352* (M); hills near Chihuahua, Chihuahua, 30 Sept. 1886, *Palmer 1075* (M); vicinity of Chihuahua, Chihuahua, alt. 1300 m., 1–21 May, 1908, *Palmer 208* (US); rocky hills near Chihuahua, Chihuahua, May, 1885, *Pringle 66* (US, G, FM); Cosihuiriachic, west of the city of Chihuahua, Chihuahua, 20 Sept. 1846, *Wislizenus 185* (M); City of Durango, Durango, 1 Aug. 1898, *Nelson 4597* (US); in the vicinity of Durango, Durango, April–Nov. 1896, *Palmer 309* (FM, US, M, G); *Palmer 930* (US, M); *Palmer 276* (US, G); Sonora, 8 Sept. 1851, *Thurber 974* (G).

16. Dyschoriste crenulata[1] n. sp. Pl, 7, fig. 2.

Stems several, 1–2 dm. high, erect or ascending from a perennial, ligneous base, pubescent; leaves more or less spathulate to obovate, 2–3 cm. long, 0.6–1 cm. broad, acute to obtuse at the apex, attenuate at the base, densely cinereous pubescent, margin crenulate; calyx 5-parted, 17–18 mm. long, nearly equalling the length of the corolla, tube and lobes of nearly equal length, lobes subulate-setaceous, cinereous, ciliate; corolla 18–19 mm. long, pubescent on the external surface, throat slightly longer than the tube; anthers occasionally unequally didynamous, style 11–12 mm. long, stigma oblique; mature capsule not seen.

Distribution: south Texas, south into Tamaulipas.

Specimens examined:

[1] **Dyschoriste crenulata** Kob., sp. nov., planta 1–2 dm. alta; caulibus pluribus, erectis vel ascendentibus a perenne lignoso basi, pubescentibus; foliis subsessilibus, plus minusve spathulatis vel plerumque obovatis, 2–3 cm. longis, 0.6–1 cm. latis, apice acutis vel obtusis, crenulatis, basi attenuatis, cinereo-pubescentibus; calyce 5-diviso, 17–18 mm. longo, prope aequante corollam, tubo lobes aequante, lobis subulato-setaceis, cinereis, ciliatis; corolla 18–19 mm. longa, extus puberula, fauce tubo paulo longiore; staminibus didynamis, subinde imperfectis; stylo pubescente, 11–12 mm. longo, stigmata obliqua; capsula ignota.—Type collected on road from "San Fernando to Jimeney," state of Tamaulipas, Mexico, 26–27 Feb., 1902, *E. W. Nelson 6604* (G).

Texas: Brazos Santiago, 1899, *Nealley 124* (*357*) (US).

Mexico: "San Fernando to Jimeney," Tamaulipas, 26–27 Feb. 1902, *Nelson 6604* (G TYPE, US isotype, M photograph and fragment).

17. **Dyschoriste capitata** (Oerst.) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891.

Calophanes capitatus Oerst. in Vidensk. Meddel. 121. 1854; Mueller in Walpers, Ann. **5:** 647. 1858; Hemsl. in Biol. Cent.-Am. Bot. **2:** 502. 1882.

Stems several, frequently branching and ascending from a ligneous base, 4 dm. high, subtetragonal, often geniculate, pubescence becoming more pronounced and flaccid near the apex; leaves obovate, 15–27 mm. long, 8–12 mm. broad, obtuse at the apex, attenuate into a petiole varying from a subsessile condition to 5 mm. in length, entire, ciliate, upper surface hirsute, especially on basal portion of midrib and petiole, sparingly so along midrib and veins of lower surface; flowers congested in heads at the apex of the stem and branches, subtended by oblanceolate bracts, the basal portion invested with long whitish hairs; calyx 9–10 mm. long, 5-lobed, joined for one-third its total length, possessing the same pubescence as the bracts, together giving a distinctly whitish appearance to the inflorescence, lobes subulate-setaceous; corolla 15–16 mm. long, puberulent on the external surface; filaments terminated by an emarginate, muticous prolongation at the apex; staminodium sometimes present; ovary glabrous, stigma linear, oblique; mature capsule glabrous, 8–9 mm. long, 4-seeded.

Distribution: mountains of southern Mexico.

Specimens examined:

Prov. of San Luis Potosi, 1851, *Oersted 808*[1] (C); Sierra de San Felipe, Oaxaca, alt. 2000 m., 15 June, 1897, *Pringle 6718* (FM, G, M, US); Valley of Oaxaca, alt. 1550 m., 8 June, 1897, *Conzatti & Gonzales 282* (G).

18. **Dyschoriste Pringlei** Greenm. in Proc. Am. Acad. **40:** 32. 1905.

[1] This citation refers to a photograph of the only Oersted specimen of *D. capitata* found in the Copenhagen Herbarium.

Stems several, 1–2 dm. in length, erect or ascending from a ligneous perennial base, densely hirsute-pubescent or subtomentose; leaves lance-elliptic to slightly obovate, 1.5–4 cm. long, 0.5–1.6 cm. broad, obtuse or acute, entire, narrowed below to a subpetiolate base, sparingly hirsute-pubescent on both surfaces; flowers crowded in the axils of the upper leaves, forming a subcapitate, leafy inflorescence; calyx 13–14 mm. long, densely pubescent with white flaccid hirsute hairs, divided to somewhat below the middle, divisions lance-attenuate; corolla tubular-campanulate, 3–4 cm. long, externally pubescent, more or less purplish-maculate, at least in the dried state; stamens adnate to the corolla for about one-half its length, anthers rather conspicuously calcarate; ovary glabrous, style pubescent; mature capsule not seen.

Distribution: southwestern Mexico.

Specimens examined:

Barranca of Rio Blanco near Guadalajara, Jalisco, alt. 1500 m., 22 July, 1902, *Pringle 11313* (G, FM, US); deep canyons near Guadalajara, Jalisco, 1 July, 1889, *Pringle 2907* (G TYPE, FM, M photograph).

19. Dyschoriste oaxacensis[1] n. sp. Pl. 10.

Stems several, procumbent, ascending from a woody base, 1–2 dm. high, pubescent with lineolations showing through pubescence; leaves sessile, oblanceolate, occasionally somewhat spathulate, 15–20 mm. long, 3–5 mm. broad, obtuse at the apex, ciliate, sparsely pubescent or glabrous, appearing scabrous because of the irregular scattering of cystoliths; flowers axillary, congested at the apex of stem and branches, producing a capitate-like inflorescence, subtended by oblanceolate bracts, approximately 10

[1] **Dyschoriste oaxacensis** Kob., sp. nov., caulibus pluribus, procumbentibus, lineolatis, 1–2 dm. altis; foliis sessilibus, oblanceolatis, rare subspathulatis, 15–20 mm. longis, 3–5 mm. latis, ciliatis, pauce pubescentibus; floribus axillaribus, in apice caulis ramorumque capitatim congestis; bracteis plus minusve 10 mm. longis; calyce 12 mm. longo, glabro, cystolithero, lobis subulatis, setaceis, ciliatis, 7 mm. longis; corolla subbilabiata, extus puberula, 20 mm. longa, tubo 7 mm. longo; antheris basi bicalcaratis; stylo lineari, pubescente, 13–14 mm. longo, stigmata lineari, obliqua; capsula 10–11 mm. longa, glabra, 4-sperma; seminibus subrotundatibus, planis, humectatis mucilaginosis.—TYPE collected on calcareous hills, Las Sedas, Oaxaca, Mexico, 9 July, 1891, *Pringle 6712* (G).

mm. long, calyx about 12 mm. long, except for the lobes glabrous and covered with cystoliths, lobes subulate-setaceous, ciliate, 7 mm. long; corolla externally puberulent, 20 mm. long, tube 7 mm. long, somewhat bilabiate; stamens adnate below the middle of the corolla limb; ovary glabrous, style 13–14 mm. long, stigma linear, oblique; mature capsule 10–11 mm. long, glabrous, 4-seeded; seeds oblique, somewhat rounded, flattened.

Distribution: southern Mexico.

Specimens examined:

Oaxaca: calcareous hills, Las Sedas, alt. 2000 m., 19 July, 1891, *Pringle 6712* (M TYPE, G, FM, US); Las Sedas, alt. 2000 m., 2 June, 1907, *L. C. Smith 419* (G); Nochixtlan, alt. 2000 m., 19 June, 1907, *Conzatti 1858* (FM).

20. Dyschoriste pinetorum[1] n. sp. Pl. 11.

Stems erect or ascending from a woody, perennial base, branches often arising from nodes of prostrate or erect growth of previous year, subquadrangular, 20–30 cm. high, nodes frequently 5–6 cm. distant, pubescent especially at the apex; leaves obovate-elliptic, 25–35 mm. long, 10–18 mm. broad, acute to subrotund at the apex, subsessile, attenuate at the base into a very short petiole, entire, ciliate, hirsute on both surfaces, the pubescence confined to midrib and veins on the under surface, veins conspicuous; flowers disposed in heads at the tips of the stems and branches and subtended by oblanceolate bracts; calyx 11–13 mm. long, divided two-thirds the distance to the base into five subulate-setaceous, ciliate lobes, pubescence similar to that of the bracts, together giving a canescent appearance to the leafy capitate inflorescence; corolla puberulent on the external surface,

[1] **Dyschoriste pinetorum** Kob., sp. nov., caulibus erectis vel ascendentibus a lignoso perenne basi, subquadrangularis, 20–30 cm. altis, nodis saepe 5–6 cm. diversis, pubescentibus praesertim apice; ramis saepe crescendentibus ex nodis prostratorum vel erectorum caulorum antecedentis anni; foliis subsessilibus, obovato-ellipticis, 25–35 mm. longis, 10–18 mm. latis, apice acutis vel subrotundis, basi in petiolum brevissimum attenuatis, integris, ciliatis, utrinque hirsutis, praesertim ad costos nervosque subtorum; floribus apice caulis ramorumque capitatim congestis; calyce 11–13 mm. longo, diviso ad ⅔ a basi in quinque subulatis, setaceis, ciliatis lobis, pubescentibus, canescentibus; corolla extus puberula, 20–21 mm. longa, tubo limbum aequante; stylo hirsuta, stigmata lineari, obliqua; capsula ignota.—Type collected in sandy fields under pines, near Patzcuaro, Michoacan, 31 July, 1892, *C. G. Pringle 4134* (G).

20–21 mm. long, tube and throat of approximately equal length; stamens adnate to about the middle of the corolla-tube; style hirsute, stigma linear, oblique; mature capsule not seen.

Distribution: southern Mexico.

Specimens examined:

Michoacan: sandy fields under pines near Patzcuaro, 31 July, 1892, *Pringle 4134* (G TYPE, isotypes in M, Ch, FM, US).

21. Dyschoriste sagittata[1] n. sp. Pl. 12.

Low-growing perennial; stems ascending 1–2 dm. high from a ligneous base, glabrous or nearly so, densely covered with cystoliths, quadrangular, somewhat winged, branched; leaves sessile, elliptic-obovate, 15–25 mm. long, 9–12 mm. broad, usually obtuse at the apex and base, glabrous, entire; bracts slender, lanceolate, glabrous, 8 mm. long, bracteoles minute, acuminate, 2–3 mm. long; calyx 8–10 mm. long, minutely pubescent on the nerves, lobes about 5 mm. long, subulate-setaceous, sparsely and minutely ciliate; corolla pubescent on the external surface, barely exceeding the calyx in length, ventricose, slightly bilabiate, lobes rounded, margins crenate; stamens small, filaments adnate to a little below the middle of the corolla-throat, anther cells converging towards the acute apex, slightly diverging at the calcarate base, giving a sagittate appearance, approximately 0.5 mm. long; style 4–5 mm. long, minutely pubescent or glabrous, stigma lobed; mature capsule not seen.

Distribution: Paraguay.

Specimens examined:

Paraguay: in region along the Alta Parana River, 1909–10, *Fiebrig 6383* (G TYPE, M fragment and photograph).

[1] **Dyschoriste sagittata** Kob. sp. nov., humilis perennis; caulibus ascendentibus, 1–2 dm. altis a lignoso basi, glabris, cystolitheris, quadrangularis, alatis, ramosis; foliis sessilibus, elliptico-obovatis, 15–25 mm. longis, 9–12 mm. latis, glabris, apice basique obtusis; bracteis angustis, lanceolatis, glabris, 8 mm. longis, bracteolis minutis, acuminatis, 2–3 mm. longis; calyce 8–10 mm. longo, puberulente in nervis loborum calycum, lobis prope 5 mm. longis, subulatis-setaceis, parce et minute ciliatis; corolla extus puberula, minor calyce paululo longiore, ventricosa, subbilabiata, lobis rotundis, marginibus crenatis; antheris sagittatis, basi divergentibus et bicalcaratis, apice acutis; stylo 4–5 mm. longo, parce pubescente vel glabro, stigmata trilobata, medio lobo longissimo, circiter 0.5 mm. longo; capsula ignota.—TYPE collected in the region along the Alta Parana River, Paraguay, coll. of 1909–10, *Fiebrig 6383* (G).

22. Dyschoriste Serpyllum (Nees) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891.

Calophanes Serpyllum Nees in Mart. Fl. Bras. **9:** 26. 1847; Nees in DC. Prodr. **11:** 110. 1847.

Stems 1 dm. or less high, erect from a suffruticose base, pubescent; lower leaves ovate, upper leaves ovate-lanceolate, narrowed at the base, 10–12 mm. long, 3–5 mm. wide, entire, glabrous, subsessile; flowers few, usually toward the apex of the stem, subtended by leafy, glabrous bracts; calyx unequally 5-parted, submembranaceous, sparsely pubescent, 12 mm. long, lobes greatly attenuated, approximately twice as long as the tube, ciliated; corolla 12–13 mm. long, pubescent on the external surface, tube very short, not more than 3–4 mm. long, ampliation into throat apparently beginning at the base of the tube; stamens abruptly yet obtusely appended at the apex, bicalcarate at the base; ovary 2-celled, each cell possessing 2 ovules, style sparsely pubescent, filiform, stigma oblique; mature capsule not seen.

Distribution: southeastern Brazil.

Specimens examined:

Brazil: in dry fields near Rio Pardo, Sept. 1826, *Riedel 45* (L TYPE, M fragment and photograph).

23. Dyschoriste Lloydii[1] n. sp. Pl. 13.

Stems branched near the base, erect, pubescent, 1–1.5 dm. high; leaves sessile, oblong-oblanceolate, 18–20 mm. long, 3–4 mm. broad, sparingly hirsute-pubescent on both surfaces, often confined to the midrib and veins, entire; bracts foliaceous, nearly equalling the calyx in length; calyx 10–10.5 mm. long, tube 4–5 mm. long, sparingly pubescent, lobes ciliate, subulate-setaceous; corolla 14 mm. long, tube 5 mm. long, approximately equalling the throat in length; ovary and stamens typical of the genus;

[1] **Dyschoriste Lloydii** Kob. sp. nov., caulibus erectis vel ascendentibus, pubescentibus, 1–1.5 dm. altis; foliis sessilibus, oblongo-oblanceolatis, 18–20 mm. longis, 3–4 mm. latis, integris, utrinque parce hirsuto-pubescentibus, praesertim ad costos nervosque; bracteis foliaceis; calyce prope 10–10.5 mm. longo, tubo 4–5 mm. longo, parum pubescente, lobis ciliatis, subulato-setaceis; corolla 14 mm. longa, tubo 5 mm. longo, prope aequante ampliatum faucem; capsula lineari, glabra, 7–8 mm. longa, 4-sperma; seminibus typicibus.—Type collected near Hacienda de Cedros, state of Zacatecas, Mexico, 1908, *F. E. Lloyd 199* (US).

capsule linear, glabrous, 7–8 mm. long, 4-seeded; seeds flattened, suborbicular, oblique.

Distribution: central Mexico.

Specimens examined:

Zacatecas: flats, Hacienda de Cedros, summer 1908, *Lloyd 199* (US TYPE).

24. **Dyschoriste microphylla** (Cav.) O. Ktze. in Rev. Gen. Pl. **2**: 486. 1891. Pl. 14.

Calophanes microphyllus (Cav.) Nees in DC. Prodr. **11**: 113. 1847; Hemsl. in Biol. Cent.-Am. Bot. **2**: 502. 1882.

Ruellia microphylla Cav. Ic. **6**: 63, *pl. 586, f. 2.* 1801; Spreng. Syst. **2**: 821. 1825.

Dyschoriste Jasminum O. Ktze. in Rev. Gen. Pl. **2**: 486. 1891.

Calophanes Jasminum-mexicanum Nees in DC. Prodr. **11**: 110–111. 1847; Hemsl. in Biol. Cent.-Am. Bot. **2**: 502. 1882.

Stem rising or ascending from a perennial base, pubescent; leaves distinctly ovate, obtuse-rotund at the apex, attenuate at the base into a petiole, 1.5–3 cm. long (including petiole), 0.9–1.2 cm. broad, glabrous except for slight pubescence on midrib and margin, entire; inflorescence terminal or on rather short lateral branches, subtended by foliaceous bracts; calyx 5-parted, 12–13 mm. long, somewhat pubescent, especially on the lobes, lobes subulate-setaceous, one-half the total length of the calyx, ciliate; corolla puberulent on the external surface, 13–14 mm. long, tube 8–9 mm. long, ampliating abruptly into the short throat, lobes rounded; stamens adnate below the center of the corolla throat, filaments broadening toward the base; style filiform, pubescent, stigma ampliated, posterior lobe rudimentary; capsule glabrous, 4-seeded, about 8 mm. long.

Distribution: southern Mexico.

Specimens examined:

Puebla: Chalmo y San Miguel, 1789–1794, *D. Luis Née* (Ma TYPE, M 928687, photograph); vicinity of Puebla at the Rancho Losado, alt. 2194 m., 29 Aug. 1909, *Bro. Nicolas 299* (US); vicinity of Puebla, date and number lacking, *Bro. Arsène* (US 1004058); Cerro Guadalupe, vicinity of Puebla, alt. 2200 m., June, 1908, *Arsène 1933* (M, G, US); entre les haciendas Santa

Barbara et Cristo, sur l'Alseseca, alt. 2150 m., 27 June, 1907, *Arséne 1528* (US); Santa Barbara, Puebla, 1 June, 1907, *Arséne 1075* (US, M).

Mexico: hills in the valley of Mexico, alt. 2500 m., 24 Aug. 1902, *Pringle 11322* (G, US).

Michoacan: vicinity of Morelia, Punguato, alt. 2100 m., 16 July, 1909, *Arséne 3044* (M, US); *Arséne 52a* (FM, US); Morelia, alt. 2000 m., 4 Aug. 1910, *Arséne* (US 1134412); vicinity of Morelia, north of Zapote, alt. 1950 m., 4 Aug. 1910, *Arséne 5728* (M, G, US); vicinity of Morelia, Cuincho, alt. 1900 m., 1 July, 1909, *Arséne 7303* (M, US).

25. **Dyschoriste saltuensis** Fernald, Proc. Am. Acad. **33**: 92. 1898.

A slender, erect, suffrutescent plant; stems branching, subtetragonal, densely covered with short appressed hairs, ciliate at the nodes; leaves lanceolate, obtuse at the tips, tapering below into a short petiole, the lower cauline, 6 cm. long, 1.5 cm. broad, the upper scarcely half as large, above covered with cystoliths, beneath strigilose-pubescent on the midrib; flowers axillary, solitary or in glomerules of 2 to 5, peduncles 3 or 4 mm. long; bracts minute; calyx hirsute, 8–10 mm. long, divided half way to the base into 5 lance-subulate lobes; corolla light purple, pubescent without, 15 mm. or less in length, the slender tube equalling the calyx and spreading into a campanulate throat; lobes oblong, truncate, 4 mm. long; filaments hirsute, style hirsute; mature capsule approximately 10 mm. long, glabrous; seeds 4, flat, oblique.

Distribution: mountains of southwestern Mexico.

Specimens examined:

Guerrero: vicinity of Acapulco, Oct. 1894–March 1895, *Palmer 506* (G TYPE, M, FM, Ch, US).

26. **Dyschoriste ciliata** (Nees) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891; Lindau in Engl. Bot. Jahrb. **19** (Beibl. 48): 15. 1894.

Calophanes ciliatus Nees in DC. Prodr. **11**: 110. 1847.

Ruellia ciliata Ruiz in DC. Prodr. **11**: 110. 1847.

Stem procumbent, glabrescent, with the apex and ascending

branches puberulent; lower leaves more or less spathulate, 3 cm. long, 1 cm. broad, upper leaves ovate to elliptic, 6–7 cm. long, 2–3 cm. broad, obtuse to acute at the apex, entire, nearly glabrous, the base cuneate-decurrent into a petiole about 1.5 cm. long; flowers axillary, in glomerules, subsessile, subtended by oblong, ciliate bracts; calyx 5-parted, 11 mm. long, joined for more than one-half the total calyx-length, lobes subulate-setaceous, ciliate; corolla infundibuliform, a little longer than the calyx; anthers slightly bicalcarate at the base.

Distribution: Peru.

Specimens examined:

Peru: near Huanuco, 1787, *Ruiz* (B TYPE, M fragment and photograph, 927773).

27. **Dyschoriste quadrangularis** (Oerst.) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891; Greenm. in Proc. Am. Acad. **33:** 487. 1898.

Calophanes quadrangularis Oerst. Vidensk. Meddel. 120. 1854; Mueller in Walpers, Ann. **5:** 647. 1858; Hemsl. in Biol. Cent.-Am. Bot. **2:** 503. 1882.

Stem erect, 8–10 dm. high, distinctly quadrangular, with ciliated wings; cystoliths especially at the swollen nodes which are quite distant; leaves ovate, oblong, 7–10 cm. long, 2–3 cm. broad, acute at the apex, attenuate at the base into a petiole, repand, crenulate; flowers verticillate, in cymose clusters at the nodes; calyx 5-parted, 11 mm. long, subtended by short, subulate bracts, tube glabrous, lineolate, equalling or a little shorter than the lobes which are subulate-setaceous, canescent-pubescent along the nerves, ciliate; corolla subbilabiate, 11 mm. long, tube slightly shorter than the limb; stamens adnate to the middle of the corolla-tube; anthers oblong with basal appendages about 0.5 mm. long, filaments accrescent at point of attachment; capsule lanceolate, 8 mm. long, 4-seeded.

Distribution: eastern Mexico.

Specimens examined:

San Luis Potosi: Los Canoas, 29 Aug. 1891, *Pringle 5020* (G).

Vera Cruz: Potrero de Consoquitla, Nov. 1841, *Liebmann* (G COTYPE); rocky soil, Zacuapan and vicinity, Oct. 1906, *Purpus 2263* (M, G, FM).

28. **Dyschoriste quitensis** (HBK.) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891; Lindau in Bull. Herb. Boiss. **5:** 679. 1897.

Calophanes quitensis (HBK.) Nees in DC. Prodr. **11:** 110. 1847.

Ruellia quitensis HBK. Nov. Gen. **2:** 240. 1817; Kunth, Syn. **2:** 37. 1837.

Stem procumbent or ascending from a woody base, 3–4 dm. high, branched, somewhat quadrangular, puberulent; leaves oblong, elliptic-lanceolate, narrowed acutely at both ends, 25–32 mm. long, 10–12 mm. broad, entire, puberulent, constricted below into a short petiole; flowers axillary, subtended by lanceolate bracts which about equal the calyx in length; calyx 5-parted, 7–8 mm. long, united for about one-half the total calyx-length, nearly as long as the corolla, lobes subulate-setaceous, quite hirsute; corolla 8–9 mm. long, pubescent on the external surface; stamens and pistils typical of the genus; mature capsule 7–8 mm. long, acute at the apex, 4-seeded; seeds typical.

Distribution: mountains of Andes, Ecuador.

Specimens examined:

Ecuador: near Quito, around Panecilli, alt. 3000 m., *Humboldt* (B TYPE, M photograph); in Andes of Ecuador, 1857–59, *Spruce 5989* (G).

29. **Dyschoriste maranhonis** (Nees) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4**^{3b}**:** 302. 1895.

Zahlbrucknera maranhonis Pohl. in Mart. Fl. Bras. **9:** 26. 1847; DC. Prodr. **11:** 108. 1847.

Calophanes maranhonis Nees in Mart. Fl. Bras. **9:** 26. 1847; Nees in DC. Prodr. **11:** 108. 1847.

Ruellia viscosa Pavon in Mart. Fl. Bras. **9:** 26. 1847; DC. Prodr. **11:** 108. 1847.

Stem ascending or erect from a perennial base, 1–1.5 dm. high, pubescent, densely so at the apex, branched; leaves oblong-oblanceolate, 20–25 mm. long, 6–8 mm. broad, obtuse at the apex, tapering to a short-petiolate base, crenulate-subrepand, lower leaves hirsute, densely so on veins of lower surface, upper leaves subtomentose; flowers axillary, subtended by lanceolate bracts; calyx usually 5-parted, 7–8 mm. long, united for about one-half

the total calyx-length, pubescent, lobes subulate-setaceous, ciliate with long flaccid hairs; corolla approximately 14 mm. long, tube gradually ampliated into the throat, pubescent on the internal as well as the external surface, occasionally only 4-lobed; stamens occasionally incompletely didynamous, the anthers sagittate, appendaged at both ends, acutely appendaged at the base; ovary glabrous, style filiform, pubescent, stigma coiled; capsule linear, 9–10 mm. long; seeds 4.

Distribution: southeastern Brazil.

Specimens examined:

Brazil: St. Ignacio, date lacking, *Sellow* (B TYPE, M fragment and photograph).

30. Dyschoriste hirsuta (Oerst.) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891.

Calophanes hirsutus Oerst. in Kjoeb. Vidensk. Meddel. 71. 1877–78.

Robust perennial, suffruticose at the base; stems erect, 4–6 dm. high, branched, at first pubescent, glabrate; leaves ovate, 15–20 mm. long, 9–12 mm. broad, subrepand, pubescent on both surfaces, petiolate, with the petiole 2–3 mm. long; flowers axillary, subtended by two oblanceolate bracts; calyx 5-parted, approximately 10 mm. long, lobes united for one-third the total calyx-length, subulate-setaceous, pubescent on the nerves, ciliate; corolla 15–16 mm. long, pale violet, pubescent on the external surface, tube and throat approximately equal in length; stamens and ovary typical of the genus.

Distribution: southeastern Brazil.

Specimens examined:

Brazil: on fields between Serra da Piedade and Lagoa Santa, 2 May, 1864, *Warming* (C TYPE, M fragment and photograph).

31. Dyschoriste hygrophiloides (Nees) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4**^{3b}: 302. 1895.

Calophanes hygrophiloides Nees in Mart. Fl. Bras. **9**: 26. 1847; Nees in DC. Prodr. **11**: 109. 1847.

Stems geniculate, ascending from a ligneous perennial base,

3–4 dm. high, pubescent; leaves petiolate, 2–3.5 cm. long, 1–2 cm. wide, lower leaves obovate-subrotund, more or less emarginate at the apex, attenuate at the base into a rather short petiole, upper leaves elliptic-ovate, softly pubescent on both surfaces, margin somewhat sinuous; inflorescence axillary, in glomerules of 2–5 flowers; bracts linear-oblanceolate, setaceous, pubescent, shorter than the calyx, resembling calyx-lobes, bracteoles present; calyx 5-parted, total length approximately 13 mm., lobes 7–8 mm. long, extremely setaceous, villous-ciliate; corolla somewhat bilabiate, puberulent on the external surface, 13–14 mm. long, tube and throat of about equal length; stamens adnate below the middle of the corolla limb, anther cells ovate; style filiform, quite pubescent, 4 mm. or less in length; stigma curved, mature capsule not seen.

Distribution: southeastern Brazil.

Specimens examined:

Brazil: in grassy fields, Parana, 10 Oct. 1914, *Dusén 15640* (G, M photograph).

32. **Dyschoriste repens** (Nees) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4^{3b}: 302. 1895.

Calophanes repens Nees in DC. Prodr. **11**: 109. 1847.

Ruellia repens Ruiz acc. to Nees in DC. Prodr. **11**: 109. 1847, in synonymy.

Stem spreading, ascending, geniculate from a perennial base, densely pubescent, branching; branches rather short, ascending, densely foliate; leaves obovate (lower) to ovate (upper), 2.5–3.5 cm. long, approximately 1 cm. broad, obtuse to acute at the apex, tapering at the base to a distinct petiole, ciliate, entire, hirsute on the upper surface, pubescence of unequal hairs on the midrib of the under surface; flowers axillary, subtended by foliaceous bracts; calyx 5-parted, 10–11 mm. long, nearly equalling the corolla, lobes united for about one-half the total length of the calyx, subulate-setaceous, conspicuously ciliate; corolla 11–12 mm. long, pubescent on the external surface, tube comparatively broad, short; ovary 2-celled, style filiform, pubescent, 6 mm. long, stigma oblique; capsule not seen.

Distribution: Peru.

Specimens examined:

Peru: "near Cheuchin," date lacking, *Ruiz* (B TYPE, M fragment and photograph).

33. Dyschoriste Pulegium (Nees) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891.

Calophanes Pulegium Nees in Mart. Fl. Bras. **9:** 25. 1847; Nees in DC. Prodr. **11:** 109. 1847.

Stem erect from a suffruticose base, subvelutinous-pubescent; leaves sessile, obovate, 2–2.5 cm. long, approximately 1 cm. broad, obtuse at the apex, tapering at the base, crenulate; flowers axillary in sessile glomerules; calyx 5-parted, 9–10 mm. long, hirsute, joined one-quarter the distance from the base, lobes subulate-setaceous, ciliate; corolla about twice the total calyx length; stamens and pistils typical of the genus; mature capsule lanceolate, 4-seeded.

Distribution: southeastern Brazil.

Specimens examined:

Brazil: date and exact locality lacking, *Sellow 173* (B TYPE, M photograph).

34. Dyschoriste ovata (Cav.) O. Ktze. Rev. Gen. Pl. **2:** 486. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4**^{3b}**:** 302. 1895; Lindau in Bull. Herb. Boiss. **5:** 678. 1897.

Calophanes ovatus Benth. in DC. Prodr. **11:** 108. 1847, as to Cavanilles plant (not Hartweg plant); Hemsl. in Biol. Cent.-Am. Bot. **2:** 502. 1882.

Ruellia ovata Cav. Ic. **3:** 28, *pl. 254*. 1794; Willd. Sp. Pl. **3:** 363. 1801.

Erect perennial, 4–6 dm. high; stems quite quadrangular, pubescent, sometimes winged, occasionally branched; leaves ovate, obovate or occasionally elliptical, 3–4 cm. long, 1–1.7 cm. broad, obtuse at the apex, attenuated at the base into a very short petiole, quite glabrous with the exception of occasional stiff hairs on the midrib and veins, cystoliths abundant, giving the appearance of appressed hairs, margin entire and ciliated, sometimes slightly repand-crenulate; flowers crowded among the foliaceous bracts at the nodes, giving a glomerulate appearance; calyx 5-parted, quite glabrous, covered with cystoliths, 14–15

mm. long, joined for about one-third the total calyx-length, lobes subulate-setaceous, ciliate; corolla 20–25 mm. long, tube less than 10 mm. long, puberulent on the external surface; stamens, pistil, and fruit typical of the genus.

Distribution: southern Mexico.

Specimens examined:

Vera Cruz: Nogales, Mt. Orizaba, alt. 1400 m., 16 Aug. 1891, *Seaton 392* (Ch, G); Borrego, near Mt. Orizaba, 26 Aug. 1866, *Bourgeau 2903* (US, G).

Morelos: near Cuernavaca, 30 July, 1906, *Pringle 13838* (US); near Cuernavaca, alt. 1500 m., 28 July, 1896, *Pringle 7249* (US).

Michoacan: Morelia, alt. 2100 m., 8 Aug. 1912, *Arsène 9027* (US).

35. **Dyschoriste amoena** (Nees) O. Ktze. Rev. Gen. Pl. **2**: 485. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4**^{3b}: 302. 1895.

Calophanes amoenus Nees in Mart. Fl. Bras. **9**: 27. 1847; Nees in DC. Prodr. **11**: 110. 1847.

Stem ascending from a perennial base, approximately 3 dm. high, geniculate, branched, puberulent toward the apex, otherwise glabrous; leaves narrowly oblong-ovate to slightly oblong-oblanceolate, 4–5 cm. long, 1–1.5 cm. broad, obtuse to acute at the apex, entire, glabrous, attenuate at the base into a very short petiole; inflorescence axillary, bracteate, glomerulate toward the apex; calyx deeply 5-parted, 2 cm. long, quite robust, pubescent, lobes less attenuate than in the majority of species, ciliate; corolla 5 mm. or more longer than the calyx, pubescent on the external surface; stamens and ovary typical of the genus; mature capsule not seen.

Distribution: southeastern Brazil.

Specimens examined:

Brazil: date and exact locality lacking, *Sellow* (B TYPE, M photograph and fragment).

36. **Dyschoriste xylopoda**[1] n. sp. Pl. 15.

[1] **Dyschoriste xylopoda** Kob., sp. nov., caulibus erectis vel ascendentibus, basi crasse lignose, 2–3 dm. altis, villoso-pubescentibus; foliis sessilibus, lanceolato-oblongis, inferioribus rare ovatis, 2.5–3.5 cm. longis, 1 cm. minusve latis, integerrimis;

Stems strict, rising from a thick woody base to a height of 2–3 dm., villous-pubescent throughout; leaves sessile or nearly so, lanceolate-oblong, or the lowermost occasionally ovate, 2.5–3.5 cm. long, approximately 1 cm. or less broad, entire; flowers 2–3 on a short peduncle in the axils of the leaves, subtended by linear-lanceolate bracts which are a little shorter than the calyx; calyx deeply 5-cleft, 17–18 mm. long, lobes 11–12 mm. long, subulate-setaceous, villous-ciliate; corolla 25–27 mm. long, pubescent on the external surface, tube 10 mm. long; stamens adnate below the middle of the corolla limb, anthers oblong-ovate, 2–3 mm. long; ovary 2-celled, glabrous, style filiform, 20 mm. long, pubescent, stigma linear, oblique, nearly 2 mm. long; mature fruit not seen.

Distribution: southern Mexico.

Specimens examined:

Jalisco: hills near Guadalajara, 19 July, 1893, *Pringle 4442* (M TYPE, G, FM).

37. **Dyschoriste oblongifolia** (Michx.) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891; Lindau in Engl. & Prantl, Nat. Pflanzenfam. **4**^{3b}: 302. 1895. Pl. 3.

Ruellia oblongifolia Michx. Fl. Bor.-Am. **2**: 23. 1805; Pursh, Fl. Am. Sept. **2**: 420. 1814.

? *Ruellia biflora* L. Sp. Pl. **2**: 635. 1753 (a doubtful synonym —refer to D. Don in Sweet's Brit. Fl. Garden).

Calophanes oblongifolia (Michx.) D. Don in Sweet, Brit. Fl. Gard. **2**: *pl. 181.* 1833; Gray, Syn. Fl. N. Am. ed 1, **2**^{1}: 324. 1878, and ed. 2, 1886; Chapman, Fl. Southeastern U.S. ed. 3, 365. 1897; Britt. & Brown, Ill. Fl. **3**: 202. 1898; Small, Fl. Southeastern U.S. ed. 1, 1083. 1903, and ed. 2, 1913.

Dipteracanthus biflorus Nees in Linnaea **16**: 294. 1842.

Dipteracanthus oblongifolius Chapman, Fl. Southeastern U.S. ed. 2, 303. 1889.

floribus 2–3, pedicellatis, axillaribus; bracteis linearo-lanceolatis, calyce haud paulo breviore; calyce profunde 5-diviso, 17–18 mm. longo, lobis 11–12 mm. longis; subulato-setaceis, villoso-ciliatis; corolla 25–27 mm. longa, extus puberulenta, tubo 10 mm. longo; filamentis basi connatis, antheris ovato-oblongis, 2–3 mm. longis; stylo 20 mm. longo, pubescente, stigmata lineari, obliqua, prope 2 cm. longa; capsula ignota. —TYPE collected on hills, near Guadalajara, Jalisco, Mexico, 19 July 1893, *C. G. Pringle 4442* (M).

Herbaceous perennial; stem quadrangular, branched at the base, erect, pubescent or softly hirsute, 4–8 dm. high; leaves sessile or short-petiolate, oblong-ovate, 2.5–4.5 cm. long, 0.5–1.5 cm. broad, rounded or obtuse at the apex, narrowed at the base, entire or slightly crenulate, softly hirsute; flowers solitary, axillary on very short pedicels, subtended by narrowly oblong, leafy bracts; calyx 15–18 mm. long, deeply 5-parted, subulate-setaceous, lobes ciliate; corolla blue, usually purple-maculate in the throat, approximately 25–27 mm. long, the tube shorter than the abruptly ampliated throat, puberulent on the external surface, lobes rounded; filaments slightly pubescent at point of adnation; anther cells oblong; mature capsule 10–12 mm. long, lanceolate; seeds 4, flattened, oblique.

Distribution: sandy pine barrens, southern Virginia to Florida.

Specimens examined:

Virginia: date and locality lacking, probably southeastern portion of the state, *Thurber* (G).

South Carolina: sandy ground, north of Graniteville, Aiken Co., 21 May, 1899, *Eggert* (M); locality lacking, May, 1867, *Ravenel* (G, US); barrens near Beaufort, Beaufort Co., 26 April, 1917, *Churchill 743* (M).

Georgia: sand hills between Grovetown and Forrest, Columbia Co., 10 June, 1902, *Harper 1312* (M, G, US); low places north of Belair, Richmond Co., 22 May, 1899, *Eggert* (M); Ocmulgee River swamp below Macon, Laurens Co., *Small* (FM); Savannah, Chatham Co., 1842, *Curtis* (M); Darien Junction, McIntosh Co., 31 May, 1909, *H. H. Smith 2219* (FM); Darien Junction, McIntosh Co., alt. sea level, 25–27 June, 1895, *Small* (FM); Lexington, Oglethorpe Co., 1836, *Short* (M).

Florida: sandy pine lands, date and exact locality lacking, *Mohr* (US 721388); eastern Florida, 1895, *Curtiss* (US); pine barrens, Duval Co., 21 April, 1902, *Fredholm 5101* (G, US); pine barrens, Duval Co., 28 April, 1902, *Fredholm 5127* (G); near Jacksonville, Duval Co., 2 May, 1893, *Curtiss 4428* (M, US); dry pine barrens, near Jacksonville, Duval Co., 8 May, 1894, *Curtiss 4667* (FM, US); Jacksonville, Duval Co., April, 1869, *Canby* (M, G, US); dry pine barrens, near Jacksonville, Duval Co., *Curtiss 1938* (M, G, US); south Jacksonville, Duval Co., 7 April,

1897, *Churchill* (G); dry sandy pine barrens, St. Augustine, St. Johns Co., May–Aug. 1875, *Reynolds* (M); sandy pine barrens, DeLand, Volusia Co., date lacking, *Harkness* (M); dry pine woods, DeLand, Volusia Co., 7 May, 1910, *Hood* (M); vicinity of Eustis, Lake Co., June–July, 1894, *Hitchcock 1454* (FM, M); Eustis, Lake Co., 26 April, 1896, *Webber 520* (M); sandy soil, high pine lands, vicinity of Eustis, Lake Co., *Nash 184* (M, G, US); Eustis, Lake Co., 28 May–15 June, 1895, *Nash 1774* (US); Winter Park, Orange Co., March, 1900, *Huger 19* (M); Clarcona, Orange Co., 18–22 Aug. 1899, *Pieters 121* (US); dry sand, Okeechobee region, Brevard Co., 2 June, 1903, *Fredholm 5870* (G); Lake City, Jefferson Co., June–July, 1898, *Hitchcock 1452, 1453* (FM); Rosewood, Levy Co., June, 1876, *Garber* (FM); dry sandy ground, Polk Co., 12 April, 1894, *Ohlinger 1415* (FM); dry land, Polk Co., 11 June, 1894, *Ohlinger 188, 1437* (FM); Lake Alfred, Polk Co., 11 June, 1922, *Armstrong & Armstrong* (M); Polk Co., March, 1890, *Milligan* (US); pine barrens, Tampa, Hillsborough Co., Aug. 1898, *Ferguson* (M); in pine lands near St. Petersburg, Pinellas Co., 10 Nov. 1907, *Deam 2832* (G); pine woods, Manatee Co., 16 March, 1887, *Rothrock* (FM 160054, 322461); sandy field, Bradentown, Manatee Co., 15 May, 1900, *Tracy 6683* (M); Fort Myers, Lee Co., 1904, *Westgate 3607* (FM); Fort Myers, Lee Co., July–Aug. 1900, *Hitchcock* (FM); Aspalaga, Liberty Co., May, 1898, *Chapman* (M).

Alabama: date and locality lacking, *Buckley* (M, US).

37a. **Dyschoriste oblongifolia** (Michx.) O. Ktze. forma **glabra** n. f.

Stem and leaves glabrous; otherwise as the species.

Distribution: Florida.

Specimens examined:

Florida: Tocoi, St. Johns Co., 1874, *Palmer 346* (M, G); Lake City, Columbia Co., 4 May, 1893, *Rolf 190* (M, FM); Gainesville, Alachua Co., 5 June, 1910, *Hood* (M); Fort Myers, Lee Co., July–Aug. 1900, *Hitchcock* (M); cypress swamp and low pine land, vicinity of Fort Myers, Lee Co., 8 May, 1916, *J. P. Standley 179* (M, G, FM, US); in pine land, Mullock Creek District, about 8 miles southeast of Fort Myers, Lee Co., May–June, 1917, *J. P. Standley 443* (M, G, FM, US); in pine land, vicinity of Fort

Myers, Lee Co., 12 May, 1916, *J. P. Standley 13* (M, G, FM, US); pine woods, vicinity of Fort Myers, Lee Co., 28 Feb. 1916, *J. P. Standley 12852* (US); vicinity of Fort Myers, Lee Co., 29 Feb. 1916, *J. P. Standley 12917* (US); moist pine lands, vicinity of Fort Myers, Lee Co., 14 Dec. 1919, *P. C. Standley 18894* (US); high pine land, Jessamine, 17–20 April, 1899, *Barnhart 2680* (FM).

38. **Dyschoriste humilis** (Griseb.) Lindau in Engl. Bot. Jahrb. **19**(Beibl. 48): 15. 1894; Lindau in Bull. Herb. Boiss. II. **3**: 628. 1903.

Ruellia geminiflora Kth. var. *humilis* Griseb. in Pl. Lor. 176. 1874, and Symb. Argent. 259. 1879.

Stem slender, branched below, ascending from a ligneous, perennial base, pubescent; leaves oblong-elliptic, 2–3.5 cm. long, 0.4–0.5 cm. broad, tapering acutely both at the apex and at the short-petiolate base, puberulent, ciliate, entire or sinuous; flowers in twos or threes, axillary, subtended by foliaceous bracts about 8–10 mm. long; calyx in anthesis approximately 14 mm. long, puberulent, lobes setaceous, 8 mm. long, at maturity the calyx sometimes attains a length of 20 mm.; corolla 21–22 mm. long, puberulent on the external surface, tube shorter than the broadly ampliated (8–9 mm. in diameter) throat; stamens adnate below the middle of the corolla throat, anther cells oblong, a little over 2 mm. long, cells of individual anthers often differing, one base distinctly acute and minutely apiculated, the other base blunt or slightly mucronate, apex of cells slightly acute; style sparsely pubescent, filiform, 19 mm. long, stigma about 2 mm. long, posterior lobe rudimentary; mature capsule exceeding the calyx lobes, 10 mm. long; retinaculum in center of each cell; seeds two, flat, oblique.

Distribution: Argentina.

Specimens examined:

Argentina: Chaco Santafichna, Mocovi, 5 Nov. 1903, *Venturi 55* (US); Cordoba, Dec. 1891, *Kuntze* (US 701502); Cordoba, 21 Dec. 1876, *Hieronymus* (FM 51116, US 282198); near the city of Cordoba, 1874–75, *Hieronymus* (FM 51115a, US 282197).

39. Dyschoriste paraguariensis[1] n. sp. Pl. 16.

Stems erect, 2–3 dm. high, strict, somewhat quadrangular, nearly glabrous, sparsely pubescent at the nodes; leaves sessile, lanceolate-elliptic, 2–2.5 cm. long, 0.5–0.8 cm. wide, acute at the apex, glabrous, covered with an irregular scattering of cystoliths, margins entire, not ciliated; flowers in twos, axillary, subtended by two foliaceous bracts which resemble the leaves in nearly every respect; calyx glabrous, except for the ciliation on the lobes, covered with a regular array of cystoliths, 14 mm. long at maturity, lobes lanceolate, setaceous, 10 mm. long; corolla approximately 18 mm. long, puberulent on the external surface, tube about 9 mm. long; style filiform, about 12 mm. long, pubescent, stigma oblique; mature capsule linear, 11–12 mm. long, glabrous, 4-seeded; seeds flattened.

Distribution: Paraguay.

Specimens examined:

Paraguay: in region of the river "Tapiraguay," Aug., *Hassler 4355* (G, TYPE).

40. Dyschoriste Tweediana (Nees) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891.

Calophanes Tweedianus Nees in DC. Prodr. **11**: 108. 1847.

Stem ascending from a perennial base, 4–6 dm. high, pubescent; leaves ovate-elliptic, 3–3.5 cm. long, 0.9–1.5 cm. broad, acute to obtuse at the apex, tapering at the base into a very short petiole, repand-subcrenate, glabrous; flowers axillary, 1–3 aggregated on very short peduncles in the axils, subtended by oblong-lanceolate bracts which are shorter than the calyx; calyx deeply 5-parted, pubescent, 14 mm. long, lobes subulate-setaceous, ciliate; corolla infundibuliform, 5-lobed, 20 mm. long, tube 8 mm. long, pubescent on the external surface, lobes ovate, obtuse; anthers

[1] **Dyschoriste paraguariensis** Kob. sp. nov., caulibus erectis, 2–3 dm. altis, strictis plus minusve quadrangularis, subglabris, parum pubescentibus ad nodos; foliis sessilibus, lanceolato-ellipticis, 2–2.5 cm. longis, 0.5–0.8 cm. latis, apice acutis, glabris, lineolatis; floribus duobus in axillaribus, bracteis duobus, foliaceis; calyce glabro, cystolithero, 14 mm. longo, lobis lanceolatis, setaceis, 10 mm. longis; corolla violacea, 18 mm. longa, extus puberula, tubo 9 mm. longo; filamentis basi connatis; stylo 12 mm. longo, piloso; capsula lineari, 11–12 mm. longa, glabra, 4-sperma; seminibus planis.—TYPE collected in the region of the river "Tapiraguay," Paraguay, Aug., *Hassler 4355* (G).

appendaged at the base, appendages connivent (according to Nees); seeds suborbicular, flattened.

Distribution: southeastern Brazil.

Specimens examined:

Brazil: in dry mountain forests in Prov. Bonar, at river Jacuhy in Rio Grande do Sul, date lacking, *Tweedie 771* (K TYPE, M photograph).

Excluded Species

Calophanes californica Rose acc. to Vasey & Rose in Contr. U.S. Nat. Herb. **1**: 85. 1890 = Ruellia californica (Rose) Johnston in Proc. Cal. Acad. Sci. IV, **12**: 1171. 1924.

Calophanes cubensis A. Rich. in Sagra, Hist. de Cuba **11**: 160. 1850 = Hygrophila brasiliensis (Spreng.) Lindau in Urb. Symb. Ant. **2**: 183. 1900.

Calophanes Palmeri Gray acc. to Watson in Proc. Am. Acad. **22**: 443. 1887 = Spigelia scabrella Benth. Pl. Hartweg. 45. 1840.

Calophanes peninsularis Rose acc. to Vasey & Rose in Contr. U. S. Nat. Herb. **1**: 75. 1890 = Ruellia peninsularis (Rose) Johnston in Proc. Cal. Acad. Sci. IV, **12**: 1172. 1924.

Dyschoriste candida Brandegee in Zoe **5**: 242. 1908 = Ruellia candida (Brandegee) Kobuski, n. comb.

Dyschoriste cubensis Urb. Symb. Ant. **7**: 381. 1912 = Apassalus cubensis (Urb.) Kobuski in Ann. Mo. Bot. Gard. **15**: 2. 1928.

Dyschoriste diffusa Urb. Symb. Ant. **7**: 380. 1912 = Apassalus diffusus (Urb.) Kobuski in Ann. Mo. Bot. Gard. **15**: 1. 1928.

Dyschoriste humistrata (Shuttl.) O. Ktze. Rev. Gen. Pl. **2**: 486. 1891 = Apassalus humistratus (Shuttl.) Kobuski in Ann. Mo. Bot. Gard. **15**: 3. 1928.

List of Exsiccatae

The distribution numbers are printed in *italics*. Unnumbered collections are indicated by a dash. The number in parentheses is the species number used in this monograph.

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Barnhart, J. H. *2680* (37a).
Bebb, R. *1348* (13).
Blumer, J. C. *2223* (15).
Bourgeau, M. *1262* (1); *2903* (34).
Britton, N. L. *155* (4).
Buckley, S. B. — (13); — (37).
Canby, W. M. — (37).
Chapman, G. W. — (37).

Churchill, J. R. —, *743* (37).
Clemens, Mr. & Mrs. J. *1069* (13).
Conzatti, C. *1521* (1); *1858* (19).
Conzatti, C. & Gonzalez, V. *282* (17).
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Curtis, M. — (37).
Curtiss, A. H. *5858* (4); *1941*, *9216* (13); —, *1938*, *4428*, *4667* (37).
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Drushel, J. A. *4136* (13).
Dugês, A. — (15).
Dusén, P. *15640* (31).
Eaton, A. A. *385*, *1247* (4).
Eggert, H. —, — (13); — (37).
Ehrenberg, K. *1223* (1).
Ferguson, A. M. — (37).
Fiebrig, K. *4856* (2); *6383* (21).
Fredholm, A. *5101*, *5127*, *5870* (37).
Gandoger, M. — (1).
Garber, A. P. — (4); — (37).
Gardner, J. *3951* (3).
Ghiesbreght, A. — (12).
Gonzalez, V. *43* (1).
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Havard, V. — (13).
Heller, A. A. *1529* (13).
Hieronymus, G. — (38).
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Hood, S. C. — (37); — (37a).
Huger, A. M. *19* (37).
Humboldt, A. — (28).
Jermy, G. *31*, *62*, *249*, *472* (13).
Jones, M. E. *374* (15).
Kuntze, O. — (38).
Lemmon, J. G. — (15).
Liebmann, F. M. — (27).
Lindheimer, F. *111*, *325*, *504*, *652*, *677*, *1063* (13).
Lloyd, F. E. *199* (23).
Maxwell, C. F. *49* (13).
Mearns, E. A. *1432* (13).
Milligan, Mrs. J. M. — (37).
Mohr, C. — (37).
Nash, G. V. *184*, *1774* (37).
Nealley, G. C. — (13); *580* (15); *124* (*357*) (16).
Née, D. L. — (24).
Nelson, E. W. *4597* (15); *6604* (16).
Nicolas, Bro. *299* (24).
Niederlein, G. *42* (8).
Oersted, A. S. *808* (17).
Ohlinger, L. B. *188*, *1415*, *1437* (37).
Orcutt, C. R. *6230* (13).
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Parry, C. C. & Palmer, Ed. *699* (15).
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Explanation of Plate

PLATE 3

Fig. 1. Flower of *D. oblongifolia* (Michx.) O. Ktze. × 3.

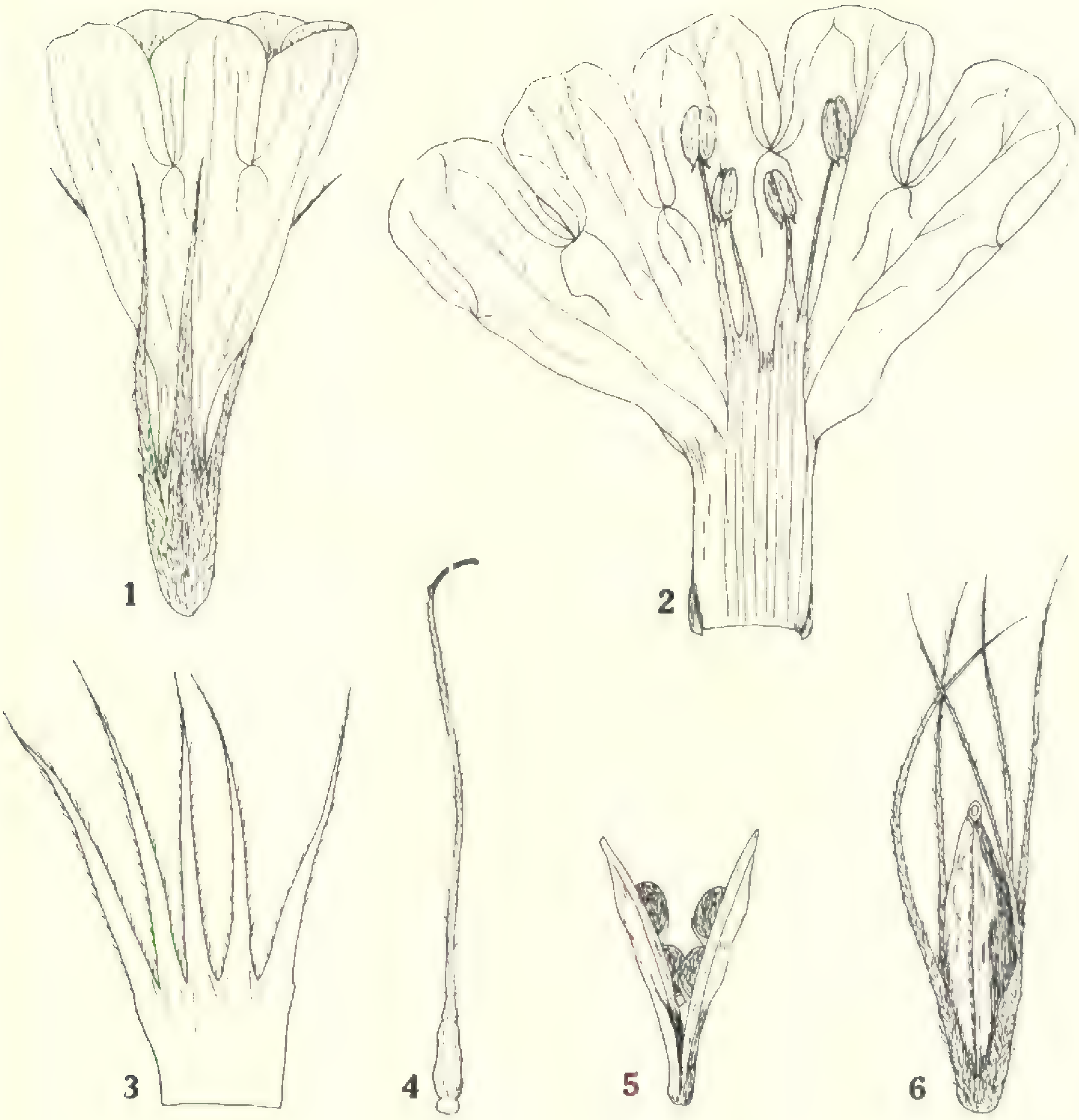
Fig. 2. Open corolla of *D. oblongifolia* (Michx.) O. Ktze. × 3. Showing character and position of stamens.

Fig. 3. Open calyx of *D. oblongifolia* (Michx.) O. Ktze. × 3.

Fig. 4. Pistil of *D. oblongifolia* (Michx.) O. Ktze. × 3.

Fig. 5. Dehiscing capsule of *D. oblongifolia* (Michx.) O. Ktze. × 3. Showing position of retinacula and seeds.

Fig. 6. Mature capsule (before dehiscence) of *D. oblongifolia* (Michx.) O. Ktze. × 3. Showing the persistent calyx.



KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 4

Dyschoriste trichanthera Kobuski

From the type specimen, *Hassler 7780,* in the Gray Herbarium of Harvard University.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 5

Dyschoriste Purpusii Kobuski

From the type specimen, *Purpus 2362*, in the herbarium of the Missouri Botanical Garden.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 6

Dyschoriste Greenmanii Kobuski

From the type specimen, *Palmer 492*, in the United States National Herbarium

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 7

Fig. 1. *Dyschoriste Rosei* Kobuski

From the type specimen, *Rose 2259*, in the United States National Herbarium

Fig. 2. *Dyschoriste crenulata* Kobuski

From the type specimen, *Nelson 6604*, in the Gray Herbarium of Harvard University.

Explanation of Plate

PLATE 8

Dyschoriste jaliscensis Kobuski

From the type specimen, *Pringle 5481*, in the Gray Herbarium of Harvard University

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 9

Dyschoriste bilabiata (Seem.) O. Ktze.

From the type specimen, *Seeman 1513*, in the Royal Botanic Gardens at Kew, England.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 10

Dyschoriste oaxacensis Kobuski

From the type specimen, *Pringle 6712*, in the herbarium of the Missouri Botanical Garden.

KOBUSKI MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 11

Dyschoriste pinetorum Kobuski

From the type specimen, *Pringle 4134*, in the Gray Herbarium of Harvard University.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 12

Dyschoriste sagittata Kobuski

From the type specimen, *Fiebrig 6383*, in the Gray Herbarium of Harvard University.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 13

Dyschoriste Lloydii Kobuski

From the type specimen, *Lloyd 199*, in the United States National Herbarium.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 14

Dyschoriste microphylla (Cav.) O. Ktze.

From the type specimen, *D. Luis Née*, in the herbarium of the Botanical Garden, Madrid, Spain.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 15

Dyschoriste xylopoda Kobuski

From the type specimen, *Pringle 4442*, in the herbarium of the Missouri Botanical Garden.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

Explanation of Plate

PLATE 16

Dyschoriste paraguariensis Kobuski

From the type specimen, *Hassler 4355*, in the Gray Herbarium of Harvard University.

KOBUSKI—MONOGRAPH OF DYSCHORISTE

STUDIES IN THE UMBELLIFERAE. I[1]

MILDRED E. MATHIAS

Jessie R. Barr Research Fellow in the Henry Shaw School of Botany of Washington University

A critical study of the genus *Cymopterus* has necessitated a detailed investigation of about twenty allied genera including *Glehnia* Schmidt.

Asa Gray in 1859 doubtfully referred a plant from the Cooper collection in the region of Puget Sound, Washington, to the genus *Cymopterus*, and in 1860 published the species as *Cymopterus* ? *littoralis.* Bentham ('67) in Bentham and Hooker's 'Genera Plantarum,' published in September, 1867, transferred this species to his new genus *Phellopterus.* F. Schmidt ('67), some time between January and July inclusive of the year 1867, in his 'Prolusio Florae Japonicae' published the new genus *Glehnia*[2] with one species, *G. littoralis,* basing it on a Maximowicz plant from Hakodate. In this work Schmidt also included *Cymopterus* ? *littoralis* Gray as a distinct species. In 1868 in his 'Flora Sachalinensis' he recognized that his *Glehnia littoralis* was conspecific with *Cymopterus* ? *littoralis* Gray and adopted the generic name *Phellopterus* of Bentham. Upon critical examination of the Cooper and Maximowicz types Schmidt's view as to the congeneric nature of the two is confirmed. As the generic name *Glehnia* of Schmidt was published at least two months prior to the *Phellopterus* of Bentham, on the basis of priority, it must be retained as the correct name for the genus and the Maximowicz plant must be taken as the generic type. The historical type of the genus is then the plant collected by Maximowicz in Hakodate, Japan, in 1861 and must bear the specific name *Glehnia littoralis* Schmidt.

Bentham, G. ('67)). In Bentham, G., and J. D. Hooker, Genera Plantarum 1: 905. September, 1867.

Gray, Asa ('59). "Botany of Japan." Mem. Am. Acad. N.S. 6[2]: 391, 428. 1859.

———, ('60). Stevens' Report of U.S. Explorations & Surveys from the Mississippi River to the Pacific Ocean 12[2]: 62. 1860.

[1] Issued April 30, 1928.

[2] The genus *Glehnia* was so named in honor of Peter von Glehn who collected with Schmidt on the Island of Sachalin.

Schmidt, F. ('67). Prolusio Florae Japonicae in Miq. Ann. Mus. Bot. Lugd. Bat. 3: 61. January–July, 1867; Prolusio Florae Japonicae, 249. 1867.

———, ('68). Flora Sachalinensis. Mem. Acad. Imp. Sci. St. Petersbourg, VII, 12²: 138–140. 1868.

Glehnia Schmidt, Prol. Fl. Jap. in Miq. Ann. Mus. Bot. Lugd. Bat. **3:** 61. Jan.–July, 1867; Prol. Fl. Jap. 249. 1867; Baillon, Hist. Plant. **7:** 215. 1880; Coult. & Rose, Contr. U. S. Nat. Herb. **7:** 165. 1900; Piper, Contr. U. S. Nat. Herb. **11:** 429. 1906; Henry, Fl. S. Brit. Col. 223. 1915; Piper & Beattie, Fl. N. W. Coast, 267. 1915; Carter & Newcombe, Prel. Cat. Fl. Vanc. 61. 1921.

Phellopterus Benth. in Benth. & Hook. Gen. Pl. **1:** 905. September, 1867, not *Phellopterus* Nutt. (section under *Cymopterus* in Torr. & Gray, Fl. N. Am. **1:** 623. 1840) in Coult. & Rose, Contr. U. S. Nat. Herb. **7:** 166. 1900; Schmidt, Mem. Acad. Imp. Sci. St. Petersbourg, VII, **12²:** 138. 1868; Franchet & Savatier, Enum. Plant. Jap. **1:** 185. 1875; Wats. Bibl. Ind. **1:** 430. 1878; Franchet, Cat. Plantes, in Mem. Soc. Nat. Sci. Cherbourg **24:** 221. 1884; Coult. & Rose, Rev. N. Am. Umbell. 21, 81. 1888; Macoun, Check List Can. Plants, 25. 1889; Cat. Can. Plants **5:** 329. 1890; Howell, Fl. N. W. Am. **1:** 259. 1898; Engl. & Prantl, Nat. Pflanzenfam. **3⁸:** 221. 1898; Ito & Matsumura, Tent. Fl. Lutch. in Jour. Coll. Sci. Imp. Univ. Tokyo **12:** 529. 1899; Yabe, Rev. Umb. Jap. in *Ibid.* **16²:** 92. 1902; Boiss. Omb. Cor. in Bull. Herb. Boiss. II, **3:** 955. 1903; Nakai, Fl. Kor. **1** in Jour. Coll. Sci. Imp. Univ. Tokyo **26¹:** 272. 1909.

Herbaceous, subacaulescent, glabrous or pubescent perennials. Leaves coriaceous, petioled, bipinnatisect, broadly ovate in general outline. Inflorescence pedunculate, villous, peduncles shorter than or equalling the leaves; involucre usually absent, sometimes present in the form of a few linear bracts; involucel of conspicuous linear-lanceolate bracts. Calyx teeth inconspicuous. Stylopodium lacking. Fruit ovate-oblong to globose, glabrous or pubescent, flattened dorsally; lateral and dorsal wings present; wings broadened at the base; oil-tubes large, numerous, 2–6 on the commissural side; strengthening cells absent.

Type species: **Glehnia littoralis** Schmidt, Prol. Fl. Jap. in Miq. Ann. Mus. Bot. Lugd. Bat. **3:** 61. 1867; Prol. Fl. Jap. 249. 1867.

Abbreviations

The following abbreviations have been used in citations to indicate the different herbaria from which material has been obtained for study:

M = Missouri Botanical Garden Herbarium; G = Gray Herbarium of Harvard University; NY = New York Botanical Garden Herbarium; US = United States National Herbarium; W = Herbarium of the University of Washington deposited in the Washington State Museum; O = Herbarium of the University of Oregon; OAC = Herbarium of the Oregon Agricultural College; C = Herbarium of the University of California; P = Herbarium of Pomona College.

Key to the Species

Fruit pubescent, species of the eastern hemisphere................*1. G. littoralis*
Fruit essentially glabrous, species of the western hemisphere........*2. G. leiocarpa*

1. Glehnia littoralis[1] Schmidt, Prol. Fl. Jap. in Miq. Ann. Mus. Bot. Lugd. Bat. **3:** 61. 1867; Prol. Fl. Jap. 249. 1867.
Pl. 17, fig. 2, 3, 5; Pl. 18; Pl. 19, fig. 1.

"*Archangelica officinalis*, Hoffm.?" in Gray, "Account of the Botanical Specimens" from Narrative of the Perry Expedition **2:** 312. 1856.

"*Cymopterus* (?) *littoralis, glaber*" Gray, "Botany of Japan," in Mem. Am. Acad. N. S. **6**[2]**:** 428. 1859, *nomen nudum.*

Cymopterus ? *littoralis* Gray, "Botany of Japan" in Mem. Am. Acad. N. S. **6**[2]**:** 391, 428. 1859, as to specimens from eastern hemisphere, *nomen nudum.*

"*Cymopteris glaber* (A. Gray)" Black, "Catalogue of Japan

[1] **Glehnia littoralis** Schmidt, em.—Planta humila, subacaula; foliis, petiolis excludentis, 5–13 cm. longis latisque, supra hirtellis in rachides nervosque, subtus glabris vel crebre tomentosis, ultimis segmentis foliorum oblongo-obovatis vel segmentis terminalibus cuneatis, 0.5–5 cm. longis, 0.4–4 cm. latis, apice rotundatis vel acutis, plus minusve cartilagineo-dentatis; petiolis 3–12 cm. longis, subdilatatis, hirtellis vel glabris; inflorescentiis umbellatis pedunculatis, crebre villosis; pedunculis subcrassis, subinde ramosis, foliis brevioribus vel aequantibus; umbellis patulis, 6–30-radiatis, radiis 1–3.5 cm. longis; involucro 1–3-bracteato; umbellulis capitatis, bracteis involucellorum pluribus, lanceolato-attenuatis; fructibus ovato-oblongis vel subglobosis, 0.4–1.5 cm. longis, villoso-pubescentibus, pilis multicellulatis; alis lateralibus saepe dorsalibus latioribus; vittis multis, 2–6 in commissurem.—Collected in Hakodate, Japan, 1861, *Maximowicz* (Gray Herb.), CO-TYPE.

Plants" in Hodgson, "A residence at Nagasaki and Hakodate in 1859–1860," 335. 1861, *nomen nudum;* Bonplandia **10:** 92. 1862, *nomen nudum.*

Phellopterus littoralis (Gray) Benth. in Benth. & Hook. Gen. Pl. **1:** 905. 1867, as to plants of eastern hemisphere; Hance, Spic. Fl. Sin. in Jour. Bot. **16:** 12. 1878; Forbes & Hemsley, Jour. Linn. Soc. Bot. **23:** 331. 1888; Engl. & Prantl, Nat. Pflanzenfam. **3**[8]: 221. 1898, as to plants of eastern hemisphere; Ito & Matsumura, Tent. Fl. Lutch. in Jour. Coll. Sci. Imp. Univ. Tokyo **12:** 529. 1899; Yabe, Rev. Umb. Jap. in *Ibid.* **16**[2]: 93. 1902; Boiss. Omb. Cor. in Bull. Herb. Boiss. II, **3:** 955. 1903; Nakai, Fl. Kor. **1.** in Jour. Coll. Sci. Imp. Univ. Tokyo **26**[1]: 272. 1909; Fl. Kor. **2.** in *Ibid.* **31:** 492. 1911.

"*C. glaber*" Gray acc. to Schmidt, Mem. Acad. Imp. Sci. St. Petersbourg, VII, **12**[2]: 139. 1868, *nomen nudum.*

"*Phellopterus littoralis*" acc. to Schmidt, Mem. Acad. Imp. Sci. St. Petersbourg, VII, **12**[2]: 138. 1868.

"*Phellopterus littoralis* Schmidt" acc. to Franchet & Savatier, Enum. Plant. Jap. **1:** 185. 1875; Franchet, Cat. Plantes, in Mem. Soc. Nat. Sci. Cherbourg **24:** 221. 1884.

"*Glehnia littoralis* (Gray) Schmidt" acc. to Coult. & Rose, Contr. U. S. Nat. Herb. **7:** 165. 1900, as to plants of eastern hemisphere.

Low subacaulescent plants; leaves, excluding petiole, 5–13 cm. long, about as broad, hirtellous on the rachises and nerves of the upper surface, glabrous to densely tomentose beneath, the ultimate leaf-segments oblong-obovate or the terminal segments cuneate, 0.5–5 cm. long, 0.4–4 cm. broad, rounded to acute at the apex, somewhat unequally cartilaginously dentate; petioles 3–12 cm. long, somewhat inflated, hirtellous to glabrous; inflorescence pedunculate, densely villous; peduncles stoutish, sometimes branched, shorter than or equalling the leaves; umbels spreading, 6–30-rayed, rays 1–3.5 cm. long; involucre 1–3-bracted; umbellets capitate, bracts of the involucel several, lance-attenuate; fruit ovate-oblong to subglobose, 0.4–1.5 cm. long, villous-pubescent with multicellular hairs, lateral wings usually broader than the dorsal wings; oil-tubes numerous, 2–6 on the commissural surface.

Type specimen: *Maximowicz,* "Glehnia littoralis F. Schmidt. Fl. Sachalin ined." Iter secundum. Japonia. Hakodate. 1861. (TYPE probably in Herb. Leningrad; CO-TYPE in the Gray Herbarium of Harvard University).

Distribution: eastern hemisphere, along sandy sea-shores, from southern China northward, and in Japan.

This plant is commonly known in Japan as "*Hama-bofu*" in relation to its maritime habitat, *hama* meaning sea-coast, and *bofu*, a medicinal plant.

Specimens examined:

JAPAN: Insula Sachalin, 1860, *Schmidt* (G); Kamiiso, Prov. Oshima, Hokkaida, 12 July, 1890, *Miyabe & Tokubuchi* (G); Hakodate, Iter secundum, 1861, *Maximowicz* (G CO-TYPE); Insula Jesso, circa Hakodate, 1861, *Albrecht* (G); Yezo, Ishikari, 10 Sept. 1903, *Arimoto* (G, M); Nambu, Nippon, 1865, *Maximowicz*, coll. Tschonoski (NY); Isoya, Shiribeshi, July, 1883, *Takenobu* (G); seashore, Prov. Rikuzen, 9 July, 1913, *Yasuda* (W); Isl. Futami, 24 June, 1910, Flora Japonica, *collector unknown* (US 1155343); Loo-Choo Islands, 1853–56, *Wright 98* (G, US); Corea, 1859, *Wilford* (NY).

SIBERIA: Vladivostok and vicinity, May–Oct. 1919, *Topping 2236* (G).

CHINA: Tsingtao, 1911, *Zimmermann* (G, US 795348); "Putoo Island—Clekiane," *Henry* (M); "Pootoo Isle, Chekiang," *Faber M*[6] (US); Delatache and Amoy, *Henry* (NY).

2. Glehnia leiocarpa[1] Mathias, nom. nov.

Pl. 17, fig. 1, 4; Pl. 19, fig. 2.

Cymopterus ? littoralis Gray, Mem. Am. Acad. N. S. **6**^{2}: 391, 428. 1859, as to American specimens, *nomen nudum;* Stevens' Rept. U. S. Expl. & Surv. from Miss. to Pacific Ocean **12**^{2}: 62. 1860; Jeps. Man. Fl. Plants Calif. 731. 1925.

Phellopterus littoralis (Gray) Benth. in Benth. & Hook. Gen.

[1] **Glehnia leiocarpa** Mathias, nom. nov.—Planta humila, subacaula; foliis, petiolis excludentis, 2.5–15 cm. longis latisque, supra hirtellis in rachides nervosque, subtus crebre tomentosis, ultimis segmentis foliorum oblongo-obovatis vel segmentis terminalibus cuneatis, 0.5–5 cm. longis, 0.4–3 cm. latis, apice rotundatis vel acutis, plus minusve dentatis, marginibus subinde cartilaginibus; petiolis 2.5–14 cm. longis, subdilatatis, hirtellis; inflorescentiis umbellatis pedunculatis, crebre villosis; pedunculis subcrassis, subinde ramosis, saepe foliis brevioribus, rare aequantibus; umbellis

Pl. **1**: 905. 1867, as to American plants; Engl. & Prantl, Nat. Pflanzenfam. **3**[8]: 221. 1898, as to American plants.

"*Glehnia littoralis* (Gray) Schmidt" acc. to Coult. & Rose, Contr. U. S. Nat. Herb. **7**: 165. 1900; Piper, Contr. U. S. Nat. Herb. **11**: 429. 1906; Piper & Beattie, Fl. N. W. Coast, 267. 1915; Carter & Newcombe, Prel. Cat. Fl. Vanc. 61. 1921.

"*Phellopterus littoralis* Schmidt" acc. to Wats. Bibl. Ind. **1**: 430. 1878; Coult. & Rose, Rev. N. Am. Umbell. 81. 1888; Macoun, Check List Can. Plants, 25. 1889; Cat. Can. Plants **5**: 329. 1890; Howell, Fl. N. W. Am. **1**: 259. 1898.

Glehnia littoralis Schmidt acc. to Henry, Fl. S. Brit. Col. 223. 1915.

Low subacaulescent plants; leaves, excluding petiole, 2.5–15 cm. long, about as broad, hirtellous on the rachises and nerves of the upper surface, mostly densely tomentose beneath, the ultimate leaf-segments oblong-obovate or the terminal segments cuneate, 0.5–5 cm. long, 0.4–3 cm. broad, rounded to acute at the apex, unequally dentate, margins sometimes cartilaginous; petioles 2.5–14 cm. long, somewhat inflated, hirtellous; inflorescence pedunculate, densely villous; peduncles stoutish, sometimes branched, usually shorter than the leaves, rarely equalling them; umbel globose to spreading, 5–13-rayed, rays 0.5–4.5 cm. long; involucre 1–3-bracted; umbellets capitate, bracts of the involucel several, lance-attenuate; fruit ovate-oblong to subglobose, 0.4–1.2 cm. long, essentially glabrous (sometimes with a few scattered multicellular hairs), lateral wings sometimes broader than dorsal wings; oil-tubes numerous, 2–6 on commissural surface.

Type specimen: *J. G. Cooper*, "sandy shores, Washington Terr. (Shoal Water Bay)." 1854. (The type is in the Gray Herbarium of Harvard University and is labeled "Cymopterus ? littoralis, n. sp." in Gray's handwriting; co-types are in the Herbarium of the New York Botanical Garden and in the United States National Herbarium.)

globosis vel patulis, 5–13-radiatis, radiis 0.5–4.5 cm. longis; involucro 1–3-bracteato; umbellulis capitatis, bracteis involucellorum pluribus, lanceolato-attenuatis; fructibus ovato-oblongis vel subglobosis, 0.4–1.2 cm. longis, fere glabris vel subinde sparse pubescentibus, pilis multicellulatis; alis lateralibus dorsalibus latioribus; vittis multis, 2–6 in commissurem.—Collected on sandy shores, Shoal Water Bay, Washington Territory (State of Washington), 1854, *J. G. Cooper* (Gray Herb.), TYPE.

Distribution: North America along sandy sea-coasts from San Francisco, California northward.

Specimens examined:

ALASKA: along the Ankow River, near Ocean Cape, vicinity of Yakutat Bay, 1 July, 1892, *Funston 51* (NY, M, C).

BRITISH COLUMBIA: vicinity of Ucleulet, Long Beach, Vancouver Island, 25 June, 1909, *Macoun 78600* (US); sand, Oak Bay, Vancouver Island, 31 May, 1887, *Macoun* (G).

WASHINGTON: Lopez, San Juan Islands, 25 June–1 Aug. 1917, *S. M. & E. B. Zeller 963* (NY, M, G, US); Puget Sound, *Wilkes Expedition* (NY, US 44092); Port Angeles, 26 June, 1908, *Webster* (W); sand dunes, Ocean Park, April, 1908, *Rigg* (W); Ilwaco, 21 June, 1904, *Piper 5002* (US); Oyhut, Chehalis County, 7 June, 1897, *Lamb 1249* (NY, M); drifting sand, common along the ocean beach, Westport, Chehalis Co., 26 June, 1892, *Henderson 385* (US); ocean beach, Westport, Chehalis County, 26 June, 1892, *Henderson* (W); sand dunes, Westport, June, 1917, *Grant* (NY); sand spit, Sequim, June, 1915, *Grant* (NY, M 788926); Seattle, July, 1915, *Freiberg* (M 813695); sandy dunes, mouth of "Joe Creek," near Moclips, 28 June, 1908, *Foster 824* (US); sandy sea-shores, Port Angeles, 26 June, 1908, *Flett 3375* (US); Olympic Mts., Clallam Co., July, 1900, *Elmer 2768* (NY, M, US); M. Beach, Westport, 10 July, 1907, *Cowles 512* (M); "sandy shores, Washington Terr. (Shoal Water Bay)." 1854, *Cooper* (G TYPE, NY, US); beach sand, Copalis, June–July, 1902, *Conrad 392* (US); Copalis, 30 May, 1912, *Bardell* (M 813656).

OREGON: Clatsop Beach, Clatsop Co., 21 Aug. 1902, *Sheldon 11252* (NY, M, G, P, US); Gearhart, 19 June, 1904, *Piper 6241* (US); Gearhart, 19 June, 1904, *Piper 6131* (US); sandy sea-beach, Newport, 3 July, 1918, *J. Nelson 2292* (G); Nestart's Bay, Tillamook Co., 29 June, 1894, *Lloyd* (NY); on strand, Nestucca, July–Aug. 1901, *Kirkwood 149* (NY); sandy sea-shore, mouth of the Umpqua River, 18 June, 1885, *Howell*[1] (OAC, US, M, 1151); on sand dunes, mouth of Tillamook Bay, 16 July, 1882, *T. Howell* (NY); on shifting sand, Tillamook Bay, 14 July,

[1] Thomas Howell in the earlier period of his botanical career used the signature Thomas J. Howell which accounts for the discrepancy in names appearing on herbarium labels.

1882, *T. J. Howell* (M, US 33339); Clatsop Beach, 26 July, 1891, *J. Howell* (M 863104); on shifting sands of sea-shore, Coos Bay, 19 Aug. 1911, *House 4705* (US, NY); drifting sand, ocean beach, Tillamook Bay, 14 July, 1882, *Howell & Henderson* (O); drifting sand, ocean beach, Clatsop, 30 July, 1887, *Henderson 385* (M, OAC); beach, below Florence, 20 May, 1925, *Henderson* (O); sand of the ocean above high tide, Rockaway, 16 Sept. 1925, *Henderson* (O); sea-shore, Fort Stevens, 7 July, 1886, *Henderson* (O); Bayocean, Garibaldi, 28 Aug. 1914, *Hitchcock 12370* (US); sands of the Oregon coast between Umpqua and Coos Bay, 12 Aug. 1880, *G. Engelmann* (M); on sand dunes of the ocean, Gearhart, Clatsop County, 1 Sept. 1898, *Coville 861* (US).

California: in drifting sand, Humboldt County, sand hills of ocean beach at Samoa, opp. Eureka, 7 Aug. 1901, *Tracy 1261* (C); Samoa Beach, Humboldt Co., 17 June, 1911, *Smith 3854* (NY); Trinidad, Humboldt Co., 7 June, 1911, *Smith 3806* (NY); Trinidad, Humboldt County, 6 July, 1911, *Smith 3806* (US); Pebble Beach, Crescent, Del Norte Co., 17–20 June, 1925, *Parks 8257* (C 279023); sandy dunes at Humboldt County camp, 7 miles south of Trinidad, 24 July, 1924, *A. A. Heller 13882* (NY); Crescent City, Del Norte Co., 30 June, 1899, *Davy & Blasdale 5960* (C); Point Arena, Mendocino Co., 24 July, 1900, *Davy 6050* (C); peninsula, Eureka, 23 Aug. 1904, *Congdon* (C 140694); sea-shore peninsula, Eureka, Humboldt Co., 23 July, 1904, *Congdon* (M); Humboldt Bay, May, 1901, *Chandler 1145* (C); Trinidad, Humboldt Co., 18 July, 1916, *Abrams 6140* (NY, O).

The genus *Glehnia* is characterized by its maritime habitat, broad leaf divisions, thick coriaceous texture of the leaves, and prominent wing development of the fruit. The two species are separated largely on fruit characters. *Glehnia littoralis* Schmidt, the species of the eastern hemisphere, always has a pubescent fruit. The pubescence is villous with multicellular hairs. The mature fruit may be only slightly pubescent due to the falling off of the hairs but in such cases it has a tuberculate appearance showing the previous attachment of these hairs. In the young fruit the pubescence is densely villous. As a rule the oil-tubes of the fruit are smaller and more numerous than in the other

species. The characters of inflorescence and foliage are similar in both species. There is quite a range of variation in foliage pubescence of *Glehnia littoralis.* The type of the species, the Maximowicz plant from Hakodate, represents an intermediate condition, and upon an examination of additional material may prove to be a hybrid between the glabrous and pubescent forms (pl. 18, fig. 2). The leaves are hirtellous on the lower surface and on the veins and rachises of the upper surface. The one extreme of variation in pubescence is typified by the plant collected by Wright in the Loo Choo Islands and labeled by Gray "Cymopterus littoralis ?? Gray, var. glabra, vel sp. aff." (pl. 18, fig. 1). The leaf is essentially glabrous, the hirtellous condition being limited entirely to the veins and rachises. The margins of the leaves are more frequently cartilaginous than in other forms. The other extreme of variation is typified by the plant collected by Schmidt in Sachalin in 1860 (pl. 19, fig. 1). This plant superficially more closely approaches the species of North America. The lower surface of the leaf has the same dense tomentose pubescence that occurs in *Glehnia leiocarpa.* However, an examination of a large amount of material from the eastern hemisphere shows a great number of intergrading forms; a gradual variation exists from the extreme glabrous form to the densely tomentose one. The fruit in all forms is similar, and the pubescence characters of the foliage are of no value in separating *Glehnia littoralis* into varieties or forms.

Glehnia leiocarpa, on the other hand, shows a very constant pubescence character. The leaves in every case are densely tomentose beneath. The fruit is glabrous with the exception of occasional multicellular hairs on the margins of the wings. In no case was a tuberculate appearance observed which would point to the previous attachment of hairs in younger conditions. The young fruit in most cases is essentially glabrous. Moreover, a cross-section of the fruit shows the oil-tubes to be larger and generally fewer in number than in *G. littoralis.*

An interesting geographical distribution is shown in connection with this genus. The two closely related species occur along the coast on both sides of the Pacific Ocean (fig. 1). *Glehnia leiocarpa* extends from Alaska to northern California and *G. littoralis* from

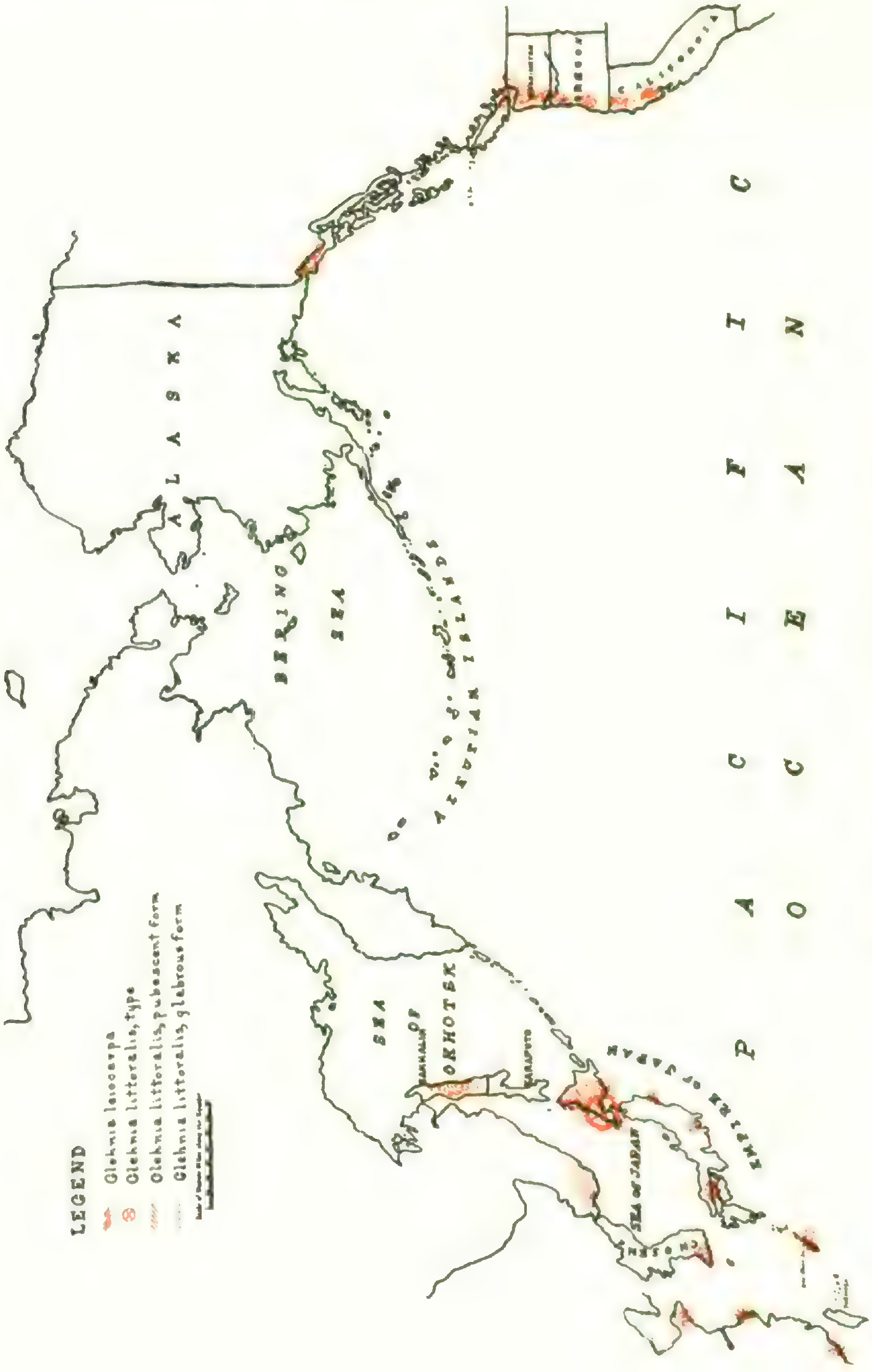


Fig. 1. Showing distrubution of species of Glehnia.

Siberia to southern China and through Japan. It is also interesting to note the distribution of the different pubescence types of *G. littoralis.* The more pubescent plants and those most nearly approaching *G. leiocarpa* occur in the northern region of the distribution area of the species, while the more glabrous plants are found in the southern range of distribution. Such a distribution seems to indicate that the ancestors of this species occurred in the intermediate area and in the land bridge connecting North America and Asia somewhere in the Bering Sea region.

A similar distribution for other genera has been pointed out by various workers in this field. One of the earliest important works was Dr. Gray's[1] article on the "Botany of Japan" in which he showed the similarity of the flora of northwest as well as eastern America to that of Japan. In this work he also mentions the distribution of the genus *Glehnia.* Butters,[2] more recently, has pointed out a similar distribution for the genus *Athyrium.* Berry[3] has shown this distribution for *Castanopsis, Pasania, Corylus, Juglans,* and other genera.

The writer is indebted to Dr. George T. Moore, Director of the Missouri Botanical Garden, for the use of the library and herbarium of that institution. Sincere appreciation is due Dr. N. L. Britton and Dr. J. K. Small of the New York Botanical Garden, Dr. B. L. Robinson and Dr. Ivan M. Johnston of the Gray Herbarium, Dr. Wm. R. Maxon of the United States National Herbarium, Prof. L. F. Henderson of the University of Oregon, Dr. Helen M. Gilkey of Oregon Agricultural College, Prof. T. C. Frye and Miss Martha R. Flahaut of the University of Washington, Dr. N. L. Gardner of the University of California, and Dr. Philip A. Munz of Pomona College for the privilege of examining material in the herbaria of the above-mentioned institutions or for the loan of material necessary for this study. Thanks are also due Dr. John H. Barnhart of the New York Botanical

[1] Gray, A. "Botany of Japan." Mem. Am. Acad. N.S. 6^2: 376–449. 1859.

[2] Butters, F. K. Taxonomic and geographic studies in North American ferns. I. The genus Athyrium and the North American ferns allied to Athyrium Filix-femina. Rhodora **19**: 169–207. 1917.

[3] Berry, E. W. Tree ancestors. 270 pp. 1923.

Garden, Dr. J. N. Rose of the United States National Herbarium, and Dr. F. A. F. C. Went of the Botanical Laboratory of Utrecht for their assistance in bibliographical details. Especial thanks are due Dr. J. M. Greenman, Curator of the Herbarium of the Missouri Botanical Garden, for his advice and assistance.

LIST OF EXSICCATAE

The distribution numbers are printed in *italics*. The number in parenthesis is the species number used in this revision.

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Arimoto, S. — (1).
Bardell, E. M. — (2).
Chandler, H. P. *1145* (2).
Congdon, J. W. — (2).
Conrad, H. S. *392* (2).
Cooper, J. G. — (2).
Coville, F. V. *861* (2).
Cowles, H. C. *512* (2).
Davy, J. B. *6050* (2).
Davy, J. B. and Blasdale, W. C. *5960* (2).
Elmer, A. D. E. *2768* (2).
Engelmann, G. — (2).
Faber, E. *M*[s] (1).
Flett, J. B. *3375* (2).
Fl. Japonica (collector unknown), — (1).
Foster, A. S. *824* (2).
Freiberg, G. W. — (2).
Funston, F. *51* (2).
Grant, J. M. — (2).
Heller, A. A. *13882* (2).
Henderson, L. F. — *385* (2).
Henry, A. — (1).
Hitchcock, A. S. *12370* (2).
House, H. D. *4705* (2).
Howell T. and Henderson, L. F. — (2).
Howell, J. — (2).
Howell, T. — (2).
Howell, T. J. — (2).
Kirkwood, J. E. *149* (2).
Lamb, F. H. *1249* (2).
Lloyd, F. E. — (2).
Macoun, J. —, 78600 (2).
Maximowicz, C. J. — (1).
Maximowicz, C. J. (coll. Tschonoski) — (1).
Miyabe, K. and Tokubuchi, E. — (1).
Nelson, J. C. *2292* (2).
Parks, H. E. *8257* (2).
Piper, C. V. *5002*, *6131*, *6241* (2).
Rigg, G. B. — (2).
Schmidt, F. — (1).
Sheldon, E. P. *11252* (2).
Smith, H. H. *3806*, *3854* (2).
Takenobu, S. — (1).
Topping, L. *2236* (1).
Tracy, J. P. *1261* (2).
Webster, E. B. — (2).
Wilford, C. — (1).
Wilkes Expedition, — (2).
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Yasuda, A. — (1).
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Zimmermann, R. — (1).

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"*Phellopterus littoralis*" acc. to Schmidt 94

Explanation of Plate

PLATE 17

Fig. 1. Mature fruit of *Glehnia leiocarpa* Mathias, collected on "sandy shores, Washington Terr. (Shoal Water Bay)," *Cooper*, 1854 (Gray Herb.), TYPE. × 6.

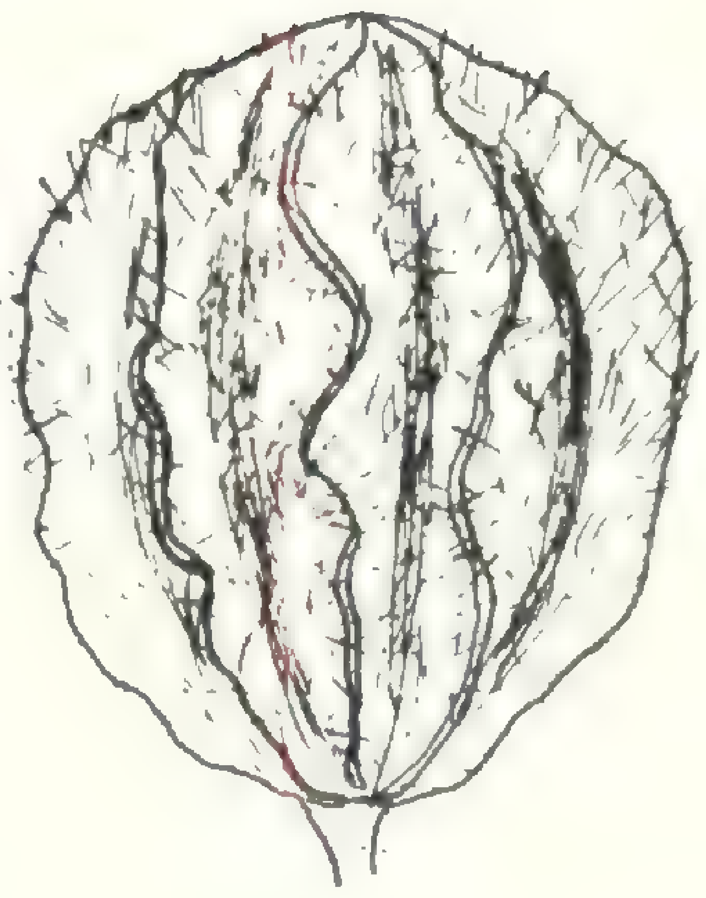
Fig. 2. Mature fruit of *Glehnia littoralis* Schmidt, collected on the Island of Sachalin, *Schmidt*, 1860 (Gray Herb.). × 6.

Fig. 3. Mature fruit of *Glehnia littoralis* Schmidt, collected in Yezo, Ishikari, *Arimoto*, 10 Sept. 1903 (Mo. Bot. Gard. Herb.). × 6.

Fig. 4. Cross-section in median plane of immature fruit of *Glehnia leiocarpa* Mathias, collected on "sandy shores, Washington Terr. (Shoal Water Bay)," *Cooper*, 1854 (Gray Herb.), TYPE. × 10.

Fig. 5. Cross-section in median plane of mature fruit of *Glehnia littoralis* Schmidt, collected on the Island of Sachalin, *Schmidt*, 1860 (Gray Herb.). × 10.

1



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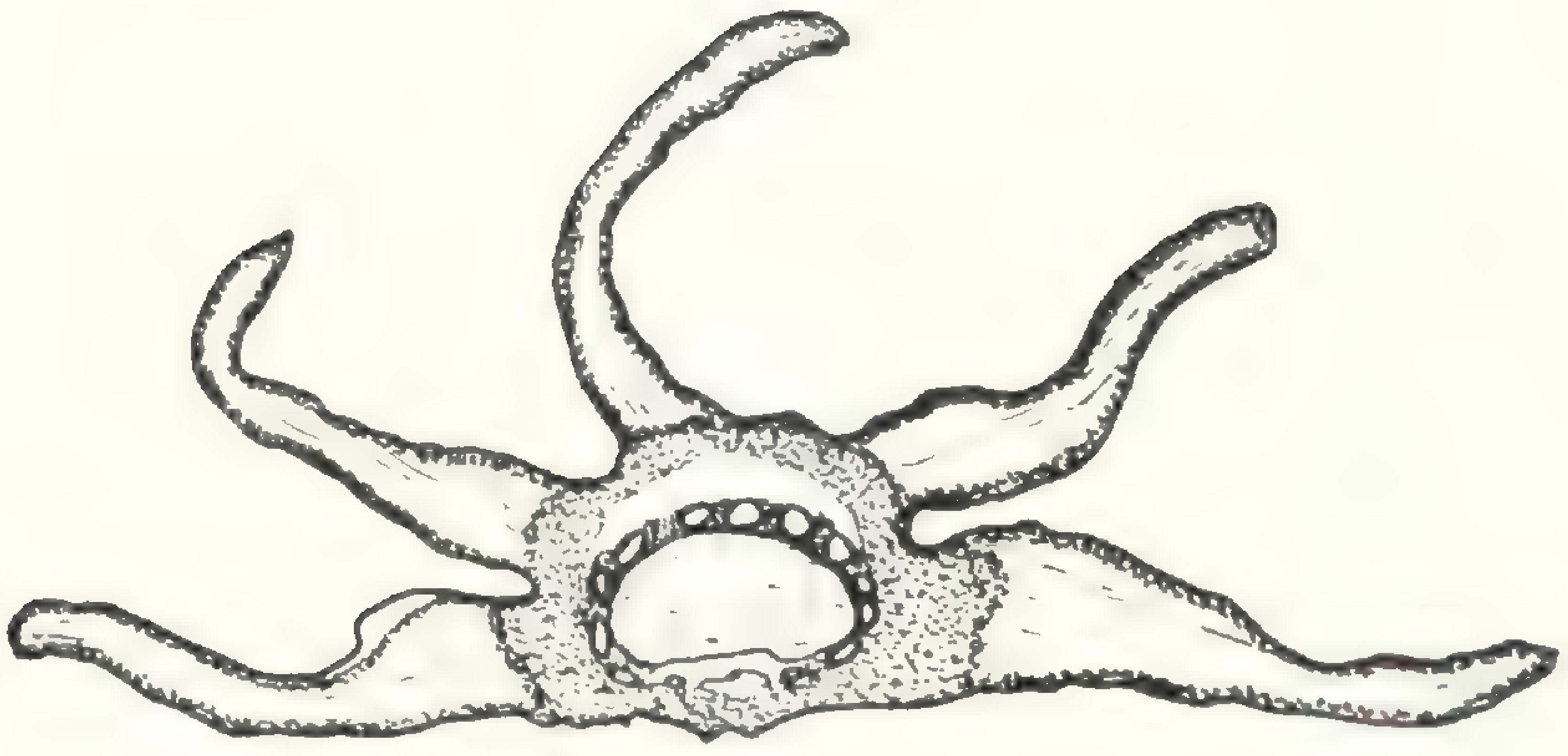

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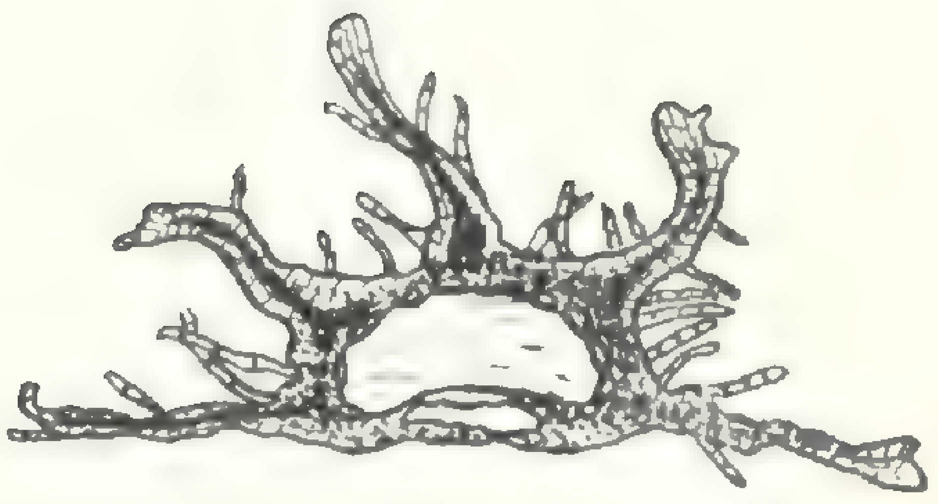

5

MATHIAS—STUDIES IN UMBELLIFERAE

Explanation of Plate

PLATE 18

Glehnia littoralis Schmidt

Fig. 1. From specimens in the Gray Herbarium of Harvard University, namely *Wright* and *Albrecht*.

Fig. 2. From the co-type specimen, *Maximowicz*, in the Gray Herbarium of Harvard University.

1

2

MATHIAS—STUDIES IN UMBELLIFERAE

Explanation of Plate

PLATE 19

Fig. 1. *Glehnia littoralis* Schmidt, from a specimen collected by *Schmidt*, in the Gray Herbarium of Harvard University.

Fig. 2. *Glehnia leiocarpa* Mathias, from the type specimen, *Cooper*, in the Gray Herbarium of Harvard University.

1

2

MATHIAS—STUDIES IN UMBELLIFERAE

CONCERNING THE STATUS OF THE GENUS LATERNEA

DAVID H. LINDER

Mycologist to the Missouri Botanical Garden
Instructor in the Henry Shaw School of Botany of Washington University

While in Cuba during the summer of 1924, the writer collected a member of the Clathreae which was subsequently determined in Saccardo ('88) as *Clathrus triscapus* (Turpin) Fr.

In going over the literature concerning the simple columnar species of *Clathrus*, it was observed that there were few statements as to the manner in which the gleba is borne. Examination of the figures accompanying the original descriptions led the writer to the conclusion that the majority of these simple species carry the gleba in the same fashion as do the more complex ones in which the columns anastomose to form a latticed sphere. In these latter forms, exemplified by *Clathrus cancellatus* and *C. crispus*, the gleba is closely applied to the inside of the columns or receptacles. However, in the genus *Laternea*, of which *L. triscapa* is the original species, the columns, strictly speaking, are stipes united above, and these subtend an angular body, subovate in outline, the "lanterne" of Turpin (1822).

A comparison of *C. columnatus*, *C. crispus*, and *C. cancellatus* brings out the fact that except for the gross morphological differences, the structure of the simple columnar and the more complex latticed species is essentially the same; that is, the columns may be relatively rough or even smooth on the outside, but on the inside they are always rough and pitted (pl. 20, figs. 3–6). It is to this pitted inside surface of the columns that the gleba is applied. Studies of preserved young material of *Clathrus columnatus* and observations of the other two species in the field at all stages of development amply support this view. There is certainly no evidence that, at the time of rupture of the volva, any definite receptacle other than the column is present.

Aside from the fact that the gleba of *Laternea triscapa* is strictly confined to the angled, subovate, specialized receptacle pendant from the junction of the apices of the columns, it differs from

C. columnatus and other similar members of that genus by being proportionately taller and more slender. In addition, the columns are less angular and the surfaces are smooth, both on the inside and outside (pl. 20, fig. 1, 2).

With the above distinction in mind, it becomes quite evident that Turpin (1822) was thoroughly justified in creating the genus *Laternea* for that form which bears the gleba in the manner mentioned. Accepting this view, then *Laternea triscapa* becomes the only representative of the genus and *Laternea columnata, L. pusilla, L. rhacoides, L. Spegazzini, L. angolensis,* and possibly *L. bicolumnata,* considered as belonging to the genus by Lloyd ('09), should be excluded and treated as members of the genus *Clathrus,* following the treatment by Fischer ('86). Certainly this is a more natural grouping, especially since *Clathrus columnatus* tends towards the more complex type represented by *C. cancellatus.* The latter species may at times be columnar below and only show anastomosis of the receptacle above, while in the former, as is shown in pl. 20, fig. 6, there is a tendency for the columns to divide to produce four or even five. If, however, it is deemed more convenient to separate the simple columnar members from the genus *Clathrus,* then the genus *Colonnaria* Rafinesque (1808), on the basis of priority, should be restored, and *Clathrus* of Michelius (1729) should be reserved for those forms with anastomosed receptacles.

In view of the former uncertainty concerning *Laternea,* it seems advisable, while restoring it to its original status, to redescribe the genus, and also the species as follows:

Laternea Turpin: Columns slender, smooth, usually three, subtending from the junction of the apices an angular, subovate receptacle to which the gleba is restricted.

Laternea triscapa Turpin: columns 3, "capucine buff"[1] at base, becoming "cadmium orange" above; smooth on inner and outer surfaces, 5–6.2 cm. long, 4–5 × 6 mm. in diameter, united above; receptacle pendant, "nopal red," angled, subovate in outline, 10 × 13 mm.; gleba deep olive; volva white, 15 × 20 mm.

In sugar cane field at edge of woods, Soledad, Cuba. Sep-

[1] Ridgway, R. Color standards and nomenclature. Washington, D. C., 1912.

tember, 1924, *Linder* (in Farlow Herb. at Harvard Univ. and writer's herbarium).

In conclusion, the writer wishes to express his indebtedness to Prof. William H. Weston, Jr. for the loan of the preserved material of *Clathrus columnatus* Bosc.

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Turpin, P. J. F. (1822). Dict. d. Sci. Nat. **25**: 248. 1822.

Explanation of Plate

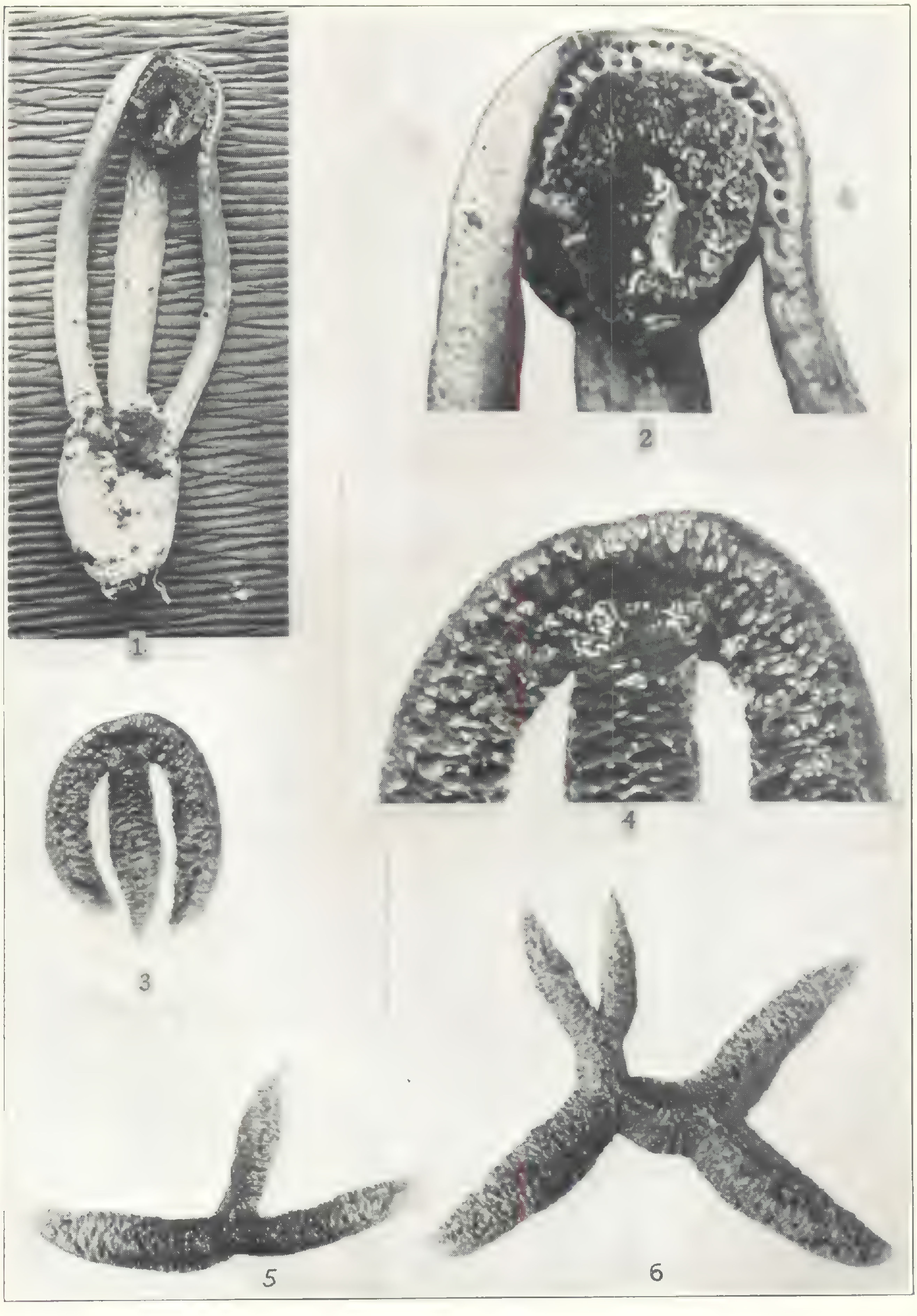
PLATE 20

Fig. 1. *Laternea triscapa*, showing the suspended, specialized receptacle bearing the gleba, and the smooth surfaces of the columns. Photograph of freshly collected specimen. Natural size.

Fig. 2. *Laternea triscapa*. Receptacle and upper part of columns enlarged three times to show the definite development of tissue to form the receptacle.

Fig. 3. *Clathrus columnatus*, showing the relatively smooth outer surface and the rough, pitted inner surface. The gleba may be seen still adhering to the inner surface at the junction of the columns or receptacles. From preserved material collected in Porto Rico by P. V. Siggers. Natural size.

Fig. 4–6. *Clathrus columnatus*. Fig. 4 shows the upper portion of the receptacle enlarged three times. There is no evidence of any tissue that may be considered comparable to that found in the receptacle of *L. triscapa*, the gleba being applied to the inner pitted surface. Figures 5 and 6 show the receptacles spread out and viewed from below; the latter figure illustrates the division of one of the columns to form a 5-columnar receptacle. $^4/_5$ natural size.



LINDER—THE GENUS LATERNEA

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SOURCES OF ENERGY FOR AZOTOBACTER, WITH SPECIAL REFERENCE TO FATTY ACIDS[1]

P. L. GAINEY

Soil Biologist, Kansas Agricultural Experiment Station
Formerly Teaching Fellow in the Henry Shaw School of Botany of Washington University

Introduction

The thermo-chemical phenomena involved in the fixation of free nitrogen by various micro-organisms are not well understood. It has been assumed that the fixation process is endothermic in nature and that the necessary energy is, in the case of the *Azotobacter* group of organisms, derived from the oxidation of organic compounds, principally of a carbohydrate, acid, or alcohol nature.

Regardless of whether the initial process through which nitrogen is brought into combination is exo- or endo-thermic, no one has been able to establish definitely a measurable fixation of nitrogen by *Azotobacter*, or any other nitrogen-fixing group of organisms, in the complete absence of some form of organic matter. Furthermore, growth and nitrogen fixation have been found to run more or less parallel with the quantity and nature of the organic material available, provided the material is non-nitrogenous in nature. It may be assumed safely, therefore, that an organic food material of some kind is essential in the metabolism of this group of organisms. This being true, it would seem highly desirable, both from a theoretical and practical standpoint, to secure as much information as possible relative

[1] An investigation carried out in part at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and in part in the Research Laboratory of Soil Biology of the Kansas Agricultural Experiment Station, and submitted as a thesis in partial fulfilment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

to the different organic food substances suitable for these organisms and also the relative efficiency with which different compounds can be used.

As an aid in the solution of some of the more complicated thermo-chemical questions involved it seemed desirable to ascertain, if possible, whether any quantitative relationship existed between the potential energy content of the organic material utilized, on the one hand, and the quantity of growth and nitrogen fixed, on the other. It was with the hope of securing information along these lines that this work was undertaken.

More specifically this investigation has been concerned with seeking an answer to the following questions: (1) Is there any difference in the relative availability of the lower fatty acids as a source of carbon, or organic food substance, for *Azotobacter?* (2) If *Azotobacter* exhibits differences in ability to utilize different fatty acids, can such differences be associated with the structure, size, or energy content of the molecule?

The following criteria were used in judging the ability of *Azotobacter* to utilize the various acids: (a) the variation in visible growth; (b) the disappearance of the acid; (c) the fixation of nitrogen; (d) changes in the hydrogen-ion concentration of the medium.

The lower fatty acids were selected for study because they compose a series of compounds exhibiting many characteristics in common, yet in the series the molecule increases in definite increments from fairly simple to fairly complex. Furthermore, the heat of combustion of these compounds increases directly as the molecular weight increases. By including the iso compounds, two molecules varying in structure but identical in composition and energy content could be compared. An additional desirable characteristic possessed by this series of compounds is that they are found as free acids or as constituents of fats in nature, and some of them are already known to serve as organic food for *Azotobacter*. One other characteristic essential in a series of compounds suitable for a study of this nature is susceptibility to fairly easy quantitative analysis. Not many series of organic compounds of which the members possess the

desirable characteristics enumerated above can be found, and possibly there is no other series in which as many members may be used so advantageously. Unfortunately, lack of solubility prevents any quantitative use of members of this series above six carbon atoms, but even then there would seem to be enough members of the series that can be used to give valuable information if carefully studied.

Methods

General procedure—The general procedure has been to prepare, in one batch, as carefully as possible, all the medium necessary for a single experiment. Measured quantities of this were placed in the culture flasks which were then stoppered with cotton and sterilized in the autoclave. After sterilization the flasks were inoculated as uniformly as possible with a heavy suspension of organisms washed from the surface of mannitol-soil-extract agar upon which active vigorous growth was taking place. No old or apparently non-vigorous growing culture was used as an inoculum. After varying periods of incubation the cultures were removed from the incubator and the qualitative and quantitative analyses were made as indicated.

Where supplementary aeration was resorted to, an inlet tube of glass, containing five to seven small openings near the end, was inserted in a rubber stopper in such a way that when the stopper was tight in the culture flask the end of the tube almost reached the bottom of the flask. The stopper was also provided with an outlet tube to be connected to a vacuum system. The stopper and connecting tubes were sterilized separately and inserted after inoculation. Cotton was forced into the ends of the connecting tubes as a precaution against possible contamination. In the aerated experiments 300-cc. Pyrex Erlenmeyer flasks were used as culture containers, and all those in any one experiment were connected in series so that the same quantity of aeration was provided for all. While incubating, a vigorous bubbling of air through the media was continuously maintained. Before entering the first culture flask the air was washed through flasks arranged as mentioned above, of acid, alkali, and water. Despite special precautions to prevent contamination there was one type of foreign organism difficult to keep out.

Where no special aeration was provided the cultures consisted of 50 cc. of media in 300-cc. flasks; 100 cc. media in 750-cc. flasks; or 200 cc. media in 1000-cc. Pyrex Erlenmeyer flasks. These quantities of media in the flasks indicated always exhibited a large surface area compared to the depth, and while aeration was certainly not as vigorous as where air was drawn through the culture, nevertheless it was ample for very rapid growth. Growth at the bottom of the culture was frequently observed before it made its appearance on the surface, indicating aeration throughout the culture. These cultures were left stationary except when being handled for examination, and even then care was taken not to shake so vigorously as to break up any film that might be forming on the surface.

Medium—Unless otherwise stated the medium used in the various experiments had the following composition, and its suitability is evidenced by the very rapid growth that took place when the organic material was assimilable:

K_2HPO_4	2.50	gms.
$MgSO_4$	.20	gm.
NaCl	.20	gm.
$CaCl_2$	.05	gm.
$FeCl_3$ (10 per cent sol.)	1.	drop
Organic material	1	per cent
Distilled water	1000	cc.

In some of the preliminary experiments only 0.50 gm. of K_2HPO_4 was used, but it was observed that when such a small quantity of phosphate was added the hydrogen-ion concentration sometimes changed so rapidly and markedly that growth was very soon inhibited by the increase of hydroxyl-ions. A rapid increase in hydroxyl-ion concentration was always observed when large quantities of a metallic salt of an organic acid were metabolized, and probably arose from the formation of an hydroxide by the metallic-ions set free when the acid radicle was assimilated by the organisms.

Even with 2.5 gms. phosphate and an excess of $CaCO_3$ the buffering effect was barely sufficient to permit of complete oxidation of 1.0 per cent acid. In fact, in some instances there is evidence to indicate that the high alkalinity accompanying vigorous oxidation not only prevented further activity, as is

evidenced by the failure of the organisms in certain cultures to oxidize all the acid even where abundant growth occurred, but actually resulted in the death of most or all of the organisms present. In case of some of the less soluble acids the quantity added was only 0.5 per cent.

When the organic material was fatty acid it was, in all except a few preliminary experiments, added to the entire volume of distilled water. An excess of $CaCO_3$ was then added, and the material boiled until the reaction became neutral to brom-thymol-blue, indicating complete transformation into the calcium salt, after which it was filtered. This procedure was resorted to in order to hasten the completion of the reaction between the weakly dissociated acid and calcium carbonate. The other salts were then added, and if any change in the reaction took place it was again adjusted to neutrality by the addition of sodium hydroxide or sulphuric acid as needed. The medium was then measured into the culture flasks, care being taken to keep it well agitated in order to secure an equal distribution of the precipitate, a small quantity of $CaCO_3$ added, the flask plugged with cotton and sterilized in the autoclave at ten pounds pressure. The final reaction of medium prepared as indicated was never far from P_H 7.0.

Obviously, one could not depend upon the original weight of any organic material subjected to the manipulations described in the preceding paragraph as indicating the final concentration. It was necessary, therefore, to prepare controls and make quantitative analyses of the final concentration of the organic materials in all cases.

The agar used for maintaining stock cultures, for testing the purity of cultures, and for the preparation of the inoculum was a soil-extract-mannitol agar prepared as follows: One thousand gms. fertile garden soil were added to 1000 cc. distilled water and subjected to fifteen pounds pressure in the autoclave for thirty minutes, after which $CaCO_3$ was added and the mixture filtered. The clear filtrate was made up to 1000 cc. with distilled water. To 900 cc. distilled water was added 100 cc. soil extract, 0.5 gm. K_2HPO_4, 10 gms. mannitol, and 15 gms. agar agar. After heating in the autoclave to bring the agar agar into

solution, and while still hot, phenolphthalein and sufficient sodium hydroxide were added to give a distinct pink color.

Cultures—The following include all cultures employed in any experiment, together with their origin. They were selected from among more than one hundred available cultures of *Azotobacter*. Those strains that were used to any appreciable extent were selected primarily because of their vigorous growing and nitrogen-fixing ability. Cultures Nos. 3a and 3b were strains of *Azotobacter chroococcum* secured from S. A. Waksman, of New Brunswick, N. J. Cultures Nos. 4, 5a, 5b, 6, 7, 8, 57, 58, 59, 60, 62, and 66 were isolated from different Colorado soils in the laboratory of W. G. Sackett, Fort Collins, Colo. Culture No. 94 was a strain of *Azotobacter vinelandii* from the Bureau of Plant Industry, U. S. Dept. Agr., Washington, D. C. Culture No. II was received from W. Omeliansky, Leningrad, Russia. Culture No. 218, a strain of *Azotobacter chroococcum* marked "K," was received from Chr. Barthel, Stockholm, Sweden. Cultures "C" and "R" were received from the Rothamsted Experiment Station, England. "C" came originally from a single cell strain of H. R. Christensen's and "R" was isolated from soil. Cultures Nos. 178, 187, 188, 194, and 165 were all isolated in this laboratory from the following soils, respectively: No. 178, Gloucester loam from Minnesota; No. 187, field soil from New York; No. 188, cotton and sugar cane soil, Virgin Islands; No. 194, soil from V. L. Winogradsky, Paris, France; No. 165, irrigated potato field soil from Wyoming. The only unidentified strain used to any appreciable extent was No. 62. This culture possessed the characteristics of *Azotobacter chroococcum* in that it grew abundantly as grayish-white opaque, distinct colonies, soon turning brown and eventually black with a more or less wrinkled dry surface.

Before any culture was used in any experiment it was carefully tested for purity by repeated streaking and re-isolation from individual, microscopically examined colonies, until assured of the presence of only one type of organism. Furthermore, after incubation most cultures were again examined for purity and if evidence of contamination was present it has been so recorded.

Inoculum.—The inoculum was prepared by streaking the

entire surface of a Kolle flask of soil-extract-mannitol agar with the desired culture, incubating 48–96 hours, or until the entire surface was covered with a uniform thick growth, and suspending this growth in 25–50 cc. of sterile water. This gave a suspension of such density as to be practically opaque in a depth of only half an inch. One or two per cent of this was used as the inoculum, thus insuring a very heavy inoculation.

Incubation.—All cultures were incubated either at summer room temperature or in an incubator at 28–32° C. Room temperature was quite favorable in the summer but during the winter the temperature dropped too low at night for active growth. Most of the aerated experiments were run at room temperature, while all non-aerated experiments were incubated at 28–32° C.

CHEMICAL METHODS

Dextrose.—Quantitative dextrose determinations were made by the Shaffer-Hartmann ('21) iodometric method. Where a heavy growth of *Azotobacter* had taken place the slime-like material present was precipitated by adding 1.0 per cent of a mixture of 2.5 gms. phosphotungstic acid and 5.0 gms. H_2SO_4 before sugar determinations were made. Preliminary experiments proved that sugar could be recovered quantitatively when added to a culture and treated by this method.

Total nitrogen.—The Gunning modification of the Kjeldahl method was employed for total nitrogen. If the culture consisted of only 50 cc. of medium the entire volume was utilized, otherwise after making the culture up to the original volume 25-cc., or more frequently 50-cc., duplicated samples were run. A small piece of copper wire, 7 gms. of anhydrous sodium sulphate, and 35 cc. H_2SO_4 were added and digestion continued for one hour after the solution became clear (see Latshaw, '16). Table I indicates the degree of accuracy with which duplicate determinations checked. In some of the experiments where aeration was employed the data for nitrogen determinations did not seem conclusive, and it has been thought best to leave them out entirely. No significance is attached to an increase in nitrogen of less than 0.5 mgs. per 100 cc. of medium, and all the data recorded in the tables are based upon 100 cc.

TABLE I

ACCURACY WITH WHICH TOTAL NITROGEN DETERMINATIONS CHECKED

Sample No.	Mgs. nitrogen recovered from		
	Peptone solution	Peptone solution	Azotobacter culture
1	9.58	9.61	2.21
2	9.52	9.52	2.34
3	9.61	9.52	2.14
4	9.58	9.58	2.21
5	9.52	9.52	2.08
6	9.52	9.58	2.27
Average	9.55	9.55	2.25

Volatile acid.—Practically all the acids used were Eastman Kodak Co. products. Quantitative determinations have been made by distilling 100 cc. from a total volume of 110 cc. Pyrex Erlenmeyer flasks of 300 cc. capacity connected to Liebig condensers and surrounded by an asbestos shield were used as distillation flasks. These were heated by an electric hot plate, and it required 30–45 minutes, depending upon the acid, to distil over 100 cc. Titrations were made in increments of 20 cc. unless it had previously been noted that practically all acid had disappeared, in which case the entire 100 cc. were titrated at one time. This fractional titration was employed in order to enable the plotting of the titration curves to detect the transformation of a higher into a lower acid. Phenolphthalein was employed as an indicator, and care was exercised that all vessels and wash water were neutralized before being used.

Figures 1 and 2 are given to show the relative titration curves of the different normal acids and also to show that there was no indication of an acid with a higher molecular weight being transformed into one of lower molecular weight. The curves for the standard acid solution and for the cultures in which abundant growth had taken place coincide as well as would curves from two different batches of acid. The culture distillation curves are from cultures in which approximately half the original acid had disappeared. Curves for iso compounds would show the same thing. These curves are plotted on a basis of the per cent of the total recovered that came over in each 20-cc. fraction, when 100 cc. were distilled from a total volume of 110 cc.

Calculations of the quantity of acid present were based upon quantitative distillations of carefully standardized acids distilled from pure water to which a small quantity of sulphuric acid had also been added. The data in table II show the per cent

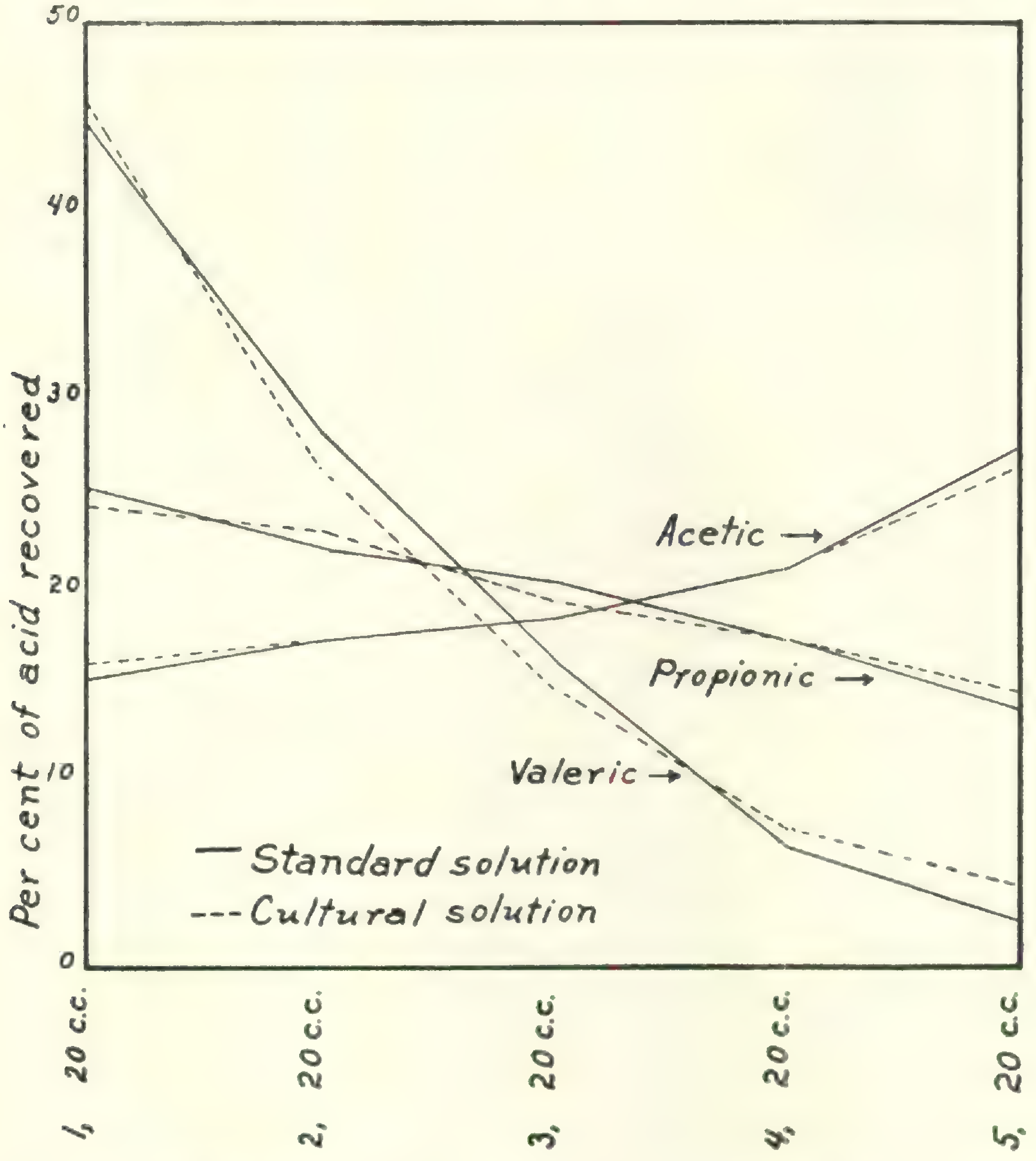

Fig. 1. Distillation curves for volatile acids from standard solutions and from cultures in which approximately half of the acid had been metabolized.

of the total recovered from the different acids when varying quantities up to 100 cc. of the total 110 cc. had been distilled. Data recorded in table III show the degree of accuracy with which triplicate determinations checked. The figures in table

IV indicate that the presence of the other constituents of the culture medium did not interfere with the recovery of the volatile acid. The quantity of medium distilled was, unless indicated to the contrary, 25 cc., and duplicate or triplicate samples were always run. Only averages of the two or three checks are

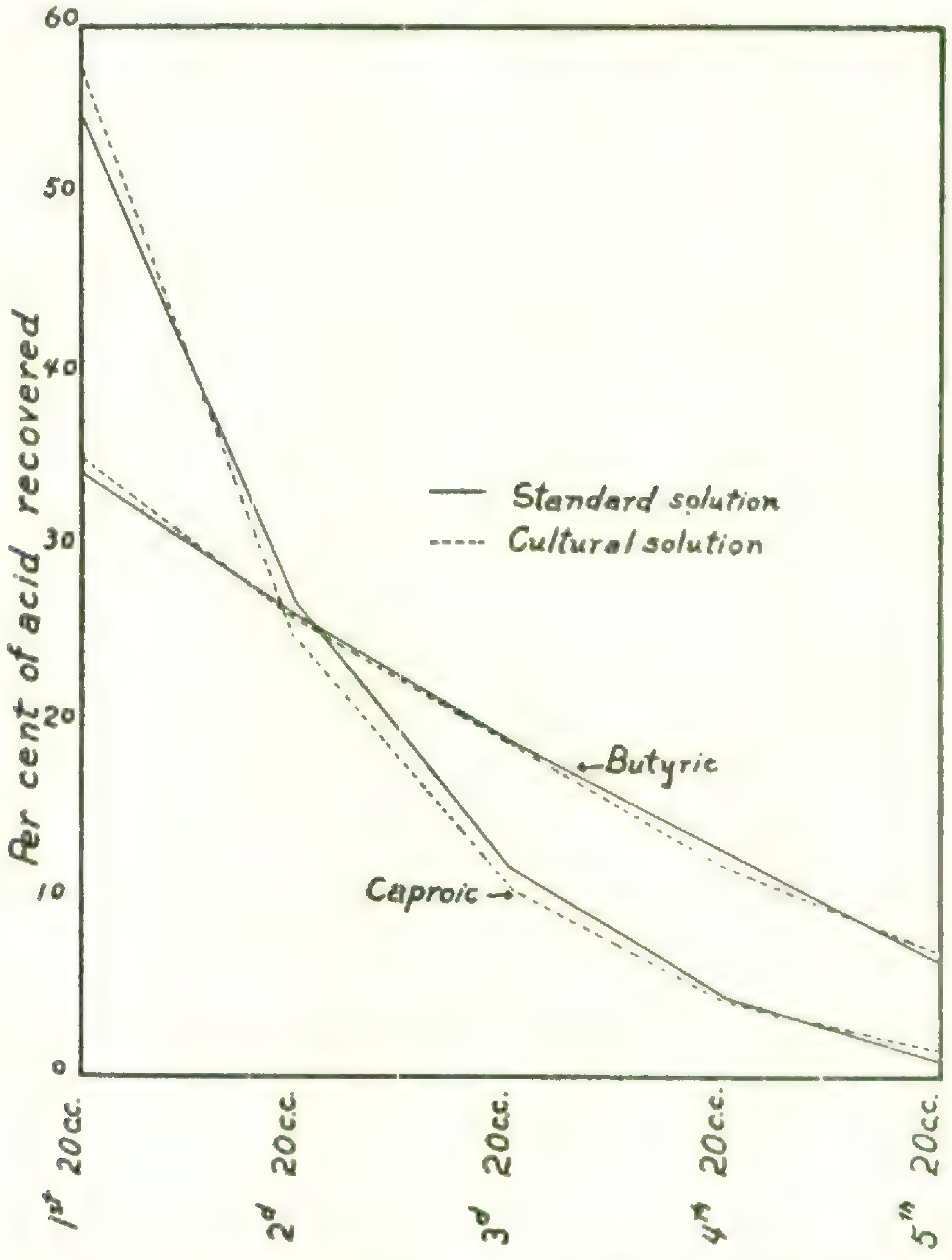

Fig. 2. Distillation curves for volatile acids from standard solutions and from cultures in which approximately half of the acid had been metabolized.

recorded. When distilled from the culture medium the volatile acid was freed from calcium by adding an excess of sulphuric acid. The CO_2 thereby liberated was removed by aerating vigorously for thirty minutes.

In the aerated cultures, run for the longer periods of time,

TABLE II

RECOVERY OF VARIOUS VOLATILE ACIDS WHEN 100 CC. WERE DISTILLED FROM A TOTAL OF 110 CC.

Cc. distilled	Per cent recovered									
	Formic	Acetic	Propionic	Normal butyric	Iso-butyric	Normal valeric	Mono-hydrated valeric	Tri-hydrated valeric	Normal caproic	Iso-caproic
20	7.3	12.5	24.2	33.5	42.7	43.9	45.5	50.7	60.4	57.8
40	15.9	26.2	45.5	59.2	70.6	71.8	72.2	77.1	88.4	84.5
60	26.2	41.3	64.9	78.0	87.5	87.9	86.2	89.7	100.0	95.6
80	40.0	58.5	81.2	90.5	95.5	94.8	93.2	97.8	100.0	100.0
100	62.2	80.8	94.4	97.2	98.9	97.4	96.1	99.4	100.0	100.0

TABLE III

THE DEGREE OF ACCURACY WITH WHICH TRIPLICATE DISTILLATIONS OF VARIOUS ACIDS COULD BE MADE

Cc. distilled	Per cent of acid recovered															
	Formic				Acetic				Propionic				Valeric			
	Flask 1	Flask 2	Flask 3	Ave.	Flask 1	Flask 2	Flask 3	Ave.	Flask 1	Flask 2	Flask 3	Ave.	Flask 1	Flask 2	Flask 3	Ave.
20	8.00	8.30	8.00	8.10	12.50	12.60	12.60	12.57	21.10	21.10	21.10	21.10	50.20	50.40	50.00	50.20
40	16.70	17.10	16.70	16.23	26.00	26.10	26.20	26.10	42.80	44.10	42.60	43.12	75.40	78.10	78.10	77.20
60	27.40	27.60	27.40	27.46	40.70	40.70	40.70	40.70	62.10	61.60	61.50	61.73	90.80	91.90	91.70	91.47
80	41.10	41.40	41.10	41.20	57.50	57.50	57.40	57.47	78.60	78.20	78.60	78.47	96.30	96.90	96.90	96.70
100	61.60	61.90	61.60	61.70	78.80	77.90	78.60	78.43	93.40	93.40	93.60	93.47	100.00	98.70	98.50	99.07

TABLE IV

RECOVERY OF ACIDS FROM PURE WATER SOLUTION AND FROM AN AZOTOBACTER CULTURE MEDIUM; EXPRESSED IN EQUIVALENT QUANTITIES OF N/20 NaOH

Cc. distilled	Butyric		Valeric		Caproic		Propionic	
	H_2O	Medium	H_2O	Medium	H_2O	Medium	H_2O	Medium
20	8.40	8.45	11.40	11.60	9.25	9.45	5.95	5.95
40	14.70	14.95	17.60	17.90	13.80	14.00	11.60	11.95
60	19.50	19.80	20.85	20.95	15.82	16.00	16.60	16.65
80	22.80	23.10	22.10	22.15	16.55	16.70	21.10	21.20
100	24.65	24.80	22.56	22.50	16.75	16.85	25.00	25.10
Total present	25.25	25.45	22.80	23.00	16.90	17.05	26.90	27.10
Per cent recovered	97.60	97.50	98.90	98.00	99.10	98.80	92.90	92.60

there were indications in some instances that slight losses of acid occurred. This is not surprising, though, in view of the fact that despite four wash-bottles, designed to remove any acids and bases that might be present in the laboratory air as well as saturate the air with moisture, there were sometimes rather large losses in the volume of culture medium. Such losses were no doubt principally due to evaporation but probably in a less degree to the mechanical removal of moisture due to the bursting of so many bubbles. Owing to such discrepancies it has been difficult to evaluate accurately the utilization of acid by the growing cultures in certain instances. We have therefore recorded as questionable such losses in the aerated experiments unless they obviously exceeded such losses where observations were possible.

Qualitative reaction.—It has been thought best to check roughly (time would not permit accurate determination) the hydrogen-ion concentration of the cultures in order to determine if the reaction were suitable for growth. For this purpose use has been made of brom-cresol-purple, brom-thymol-blue, phenol-red, cresol-red, phenolphthalein, and thymol-blue. Since the medium was only tested roughly as to whether it was acid, alkaline, or neutral to those indicators within whose range its reaction lay, the figures recorded in the various tables are merely approximate. Only in those instances where the medium was found to be alkaline to thymol-blue and is recorded as 9.0 + has there been any indication that the reaction was unfavorable. In all

probability a medium alkaline to thymol-blue has an unfavorable, if not toxic, effect upon *Azotobacter* (see Johnson and Lipman, '22).

Preliminary Experiments

A large number of experiments of a preliminary nature have been performed. In fact, before any method, or step in a method, or culture was adopted for experimental use it was carefully tried to see that it would work satisfactorily. Among these preliminary experiments there are, aside from those already mentioned, a number that seem to be of sufficient significance to record.

Experiments reported by Hunter ('23) indicated that by drawing a current of air through the medium, growth of *Azotobacter* and fixation of nitrogen could be greatly stimulated. Since the use of any method that would hasten growth seemed desirable, in view of the slow assimilation of certain of the fatty acids reported by Mockeridge ('15), it was thought that Hunter's method might be used advantageously. Therefore, an experiment was designed not only to confirm Hunter's results but at the same time to determine whether varying the rate of aeration would influence quantitatively the consumption of the organic food and the fixation of nitrogen. The results of such an experiment are reported in table v.

No method of measuring quantitatively the rate of flow of air through the medium was available; however, in the samples subjected to "slow" aeration a slow continuous flow of bubbles, perhaps one a second, was maintained. In the "medium" aerated cultures the air was drawn through at least ten times as rapidly, while the cultures subjected to "rapid" aeration probably received ten times as much air as the "medium" aerated cultures.

The data show very definitely that increasing the rate of aeration increases both the rate of dextrose consumption and nitrogen fixation. There is some indication that the dextrose may possibly be utilized somewhat more efficiently with limited aeration, the average nitrogen-dextrose ratio being 1 : 79 for the "slow" aerated samples, whereas the corresponding ratio for the other samples was 1 : 115 and 1:113 respectively.

TABLE V

EFFECT OF AERATION UPON THE UTILIZATION OF DEXTROSE AND THE FIXATION OF NITROGEN BY CULTURE NO. 3A. INCUBATION 4 DAYS

Flask No.	Aeration "slow"			Aeration "medium"			Aeration "rapid"		
	Mgs. dextrose consumed	Mgs. nitrogen fixed	Mgs. dextrose per mg. nitrogen fixed	Mgs. dextrose consumed	Mgs. nitrogen fixed	Mgs. dextrose per mg. nitrogen fixed	Mgs. dextrose consumed	Mgs. nitrogen fixed	Mgs. dextrose per mg. nitrogen fixed
1	104	1.38	75	622	5.37	116	954	8.82	108
2	108	1.24	87	693	5.64	123	954	8.41	113
3	108	1.52	71	606	4.82	126	954	8.27	115
4	96	1.38	70	690	6.85	101	954	8.27	115
5	112	1.24	90	412	3.45	119	954	8.41	113
Average	105	1.35	79	605	5.25	115	954	8.44	113

In this connection it might be well to comment, in passing, upon the use of the term "dextrose-nitrogen ratio." Certain investigators in speaking of this relationship have made use of the term "carbon-nitrogen ratio." This term, it is believed, does not accurately express the relationship. If it is a question of the organism securing or setting free a certain quantity of energy per unit of carbon, as is usually considered, obviously the expression C : N ratio is incorrect in that the energy freed per unit of carbon depends upon the other elements combined with the carbon as well as upon the carbon. For example, caproic acid contains approximately twice as much energy per gram of material and one and one-fourth times as much energy per gram of carbon as does dextrose, both being six carbon atom compounds. It would seem, therefore, that it would be much more logical to express this relationship upon an energy or molecular basis.

In an effort to secure a desirable culture with which to carry out the more extensive investigations recorded in the next part of this paper, the experiments reported in tables VI and VII were designed. All the cultures available at that time were included in these tests.

TABLE VI

VARIATION IN UTILIZATION OF DEXTROSE AND FIXATION OF NITROGEN BY DIFFERENT CULTURES OF AZOTOBACTER

Culture No.	Incubation 2 days			Incubation 5 days		
	Mgs. dextrose consumed	Mgs. nitrogen fixed	Mgs. dextrose per mg. nitrogen fixed	Mgs. dextrose consumed	Mgs. nitrogen fixed	Mgs. dextrose per mg. nitrogen fixed
3a	169	2.20	77	620	4.96	125
3b	197	2.48	79	674	6.06	111
4	171	1.38	124	522	1.10	474
5a	179	2.06	82	679	3.58	189
5b	169	2.34	72	729	3.58	203
6	247	2.34	106	692	3.04	227
7	157	.82	192	250	.82	610
8	148	1.38	107	368	1.66	222

These data indicate that culture No. 3a was approximately as efficient in fixing nitrogen as any other. At the same time

TABLE VII

UTILIZATION OF DEXTROSE AND NORMAL BUTYRIC ACID* AND FIXATION OF NITROGEN BY DIFFERENT CULTURES OF AZOTOBACTER

Culture No.	Mgs. dextrose utilized	Mgs. nitrogen fixed	Mgs. dextrose used per mg. nitrogen fixed	Mgs. butyric acid utilized	Mgs. nitrogen fixed	Mgs. butyric acid used per mg. nitrogen fixed
3a	957	5.40	177	99	1.38	72
3b	957	4.55	210	98	1.76	55
4	84	.50	168	3	.00	—
5a	957	5.40	177	96	1.65	58
5b	957	6.20	154	99	1.24	80
6	620	3.02	208	99	1.38	72
7	84	.28	300	0	.00	—
8	957	3.44	284	99	.82	121

* Butyric acid neutralized with sodium hydroxide.

it grew abundantly, thus enabling ready detection of growth. It was also known to be a strain of *Azotobacter chroococcum*. For these reasons it was temporarily selected for further study.

These data also indicate that certain cultures (Nos. 4 and 7), to all appearance *Azotobacter*, developed very poorly in the dextrose and not at all in the butyric acid medium. When measured by the quantity of nitrogen fixed per unit of organic material used, the actively growing cultures were apparently capable of utilizing butyric acid much more effectively than dextrose. In this particular experiment the increased effectiveness with which butyric acid was used might have been due to the relatively low per cent present, compared with dextrose. It has been frequently observed that in the presence of small quantities of organic material a higher fixation of nitrogen takes place per unit of organic material consumed. In this experiment only 0.1 per cent butyric acid was present.

Having selected culture No. 3a the next step was to test it in a preliminary way with several acids. Accordingly, the experiment recorded in table VIII was arranged. For some unknown reason this culture was only able to utilize acetic acid among those tested. Similar results were secured in other experiments.

Other cultures having been added to our collection, further qualitative tests were carried out, among which was the protocol

TABLE VIII

UTILIZATION OF VARIOUS ACIDS BY CULTURE NO. 3A

Acid	Mgs. recovered per 100 cc. culture solution					
	Controls		Incubation period in days			
	Unaerated	Aerated	2	5	9	13
Formic	644	696	716	659	635	673
Acetic	1026	977	982	431	394	264
Propionic	1051	——	998	996	1002	996
Butyric	1018	1001	994	984	997	1001
Valeric	920	896	896	884	875	884
Dextrose	934	954	690	423	000	000

arranged in table IX. This experiment was also designed to gain some information relative to the effect of the cation as well as the acid radicle. The salts included were the only ones available of those particular acids at that time.

The results presented in table IX indicate very strongly that the cation is probably of as much significance in determining the availability of an acid as is the anion. None of the formates permitted growth. This has been characteristic of formic acid in all tests conducted with it and is probably due to the formation of formaldehyde. Aluminum acetate appears to be the most readily available salt of acetic acid tested, all the strains being able to assimilate it readily. Uranium acetate, on the other hand, was not assimilated by any of the cultures. Between aluminum and uranium lay calcium, ammonium, magnesium, potassium, and sodium salts, their availability being approximately in the order given.

Ammonium acetate, while apparently assimilated by all ten cultures, supported vigorous growth only in two instances. It is possible that when supplied with nitrogen the very small quantities of organic impurities finding their way into the cultures enabled the various cultures to make perceptible growth. This, though, does not seem probable. Only half the cultures were capable of making visible growth when the sodium salt was the only source of organic matter supplied, and only one out of the ten assimilated it readily. Culture No. 60 could not even metabolize dextrose readily.

This experiment, as well as others reported in this paper,

TABLE IX

UTILIZATION OF VARIOUS SALTS OF FORMIC AND ACETIC ACIDS BY DIFFERENT CULTURES OF AZOTOBACTER. INCUBATED 48 DAYS

Culture No.	Ammonium formate	Calcium formate	Sodium formate	Ammonium acetate	Aluminum acetate	Calcium acetate	Magnesium acetate	Potassium acetate	Sodium acetate	Uranium acetate	Dextrose
3a	—*	—	—	+	+++	+++	+	+	+	—	+++
4	—	—	—	+	+++	+++	?	—	—	—	+++
5a	—	—	—	+++	+++	+++	+++	+	+	—	+++
6	—	—	—	+	+++	+++	+++	+	+	—	+++
57	—	—	—	+++	+++	+++	+++	+	—	—	++
58a	—	—	—	+	+++	+	?	?	—	—	+
59	—	—	—	+	+++	+++	+	+	+	—	+++
60	—	—	—	+	+++	?	?	?	—	—	—
62	—	—	—	+	+++	+++	+++	+	+++	—	++
66	—	—	—	+	+++	+++	?	—	—	—	++

* In this and all succeeding tables a minus sign indicates no growth; a question mark indicates questionable growth; while the number of plus signs indicate the relative growth observed in that particular experiment. (The same number of plus signs indicate more or less comparable growth in different experiments.)

indicates a very wide variability in the metabolism of organisms belonging to the genus *Azotobacter.* The data also emphasize the great need for more specific physiological studies of this very interesting group of organisms. It would appear utterly futile to attempt to apply the findings from the study of one strain or species to any other strain or species. Just as Löhnis and Smith ('16) have pointed out the futility of attempting to apply the morphological findings in any particular medium or at any particular time to the group as a whole, it is well to emphasize the same with regard to physiological studies.

Since culture No. 62, apparently a strain of *Azotobacter chroococcum* and hence very closely related to culture No. 3a, seemed from the above-reported experiment, as well as from a number of unrecorded tests, to possess the ability to utilize a wider variety of salts of fatty acids than any other available culture, it was selected for the more intense studies reported in the next part of this paper. Also, even though aluminum acetate was undoubtedly more readily available to some strains of *Azotobacter* than the calcium salt, the latter served equally as well for culture No. 62; and since calcium salts have found a much wider use in biological studies than aluminum it seemed desirable to use the calcium salt, thus making any results that might be secured more comparable with those reported by others. In addition, calcium salts are somewhat more easily prepared than aluminum. Calcium was therefore used as the basic element in succeeding studies.

The question of the influence of the cation should certainly receive more study, and it is hoped that such studies may be continued in the near future. The data presented in table IX are only indicative of what may be expected.

Experiments with Culture No. 62

As previously mentioned, culture No. 62 probably belonged to the species *Azotobacter chroococcum.* Preliminary experiments indicated that it was a vigorously growing and strong nitrogen-fixing strain when supplied with a suitable form of organic material such as dextrose and certain of the lower fatty acids. The experiments conducted with this culture were all aerated.

Aeration was employed because the work of Mockeridge ('15) indicated that the rate at which certain organic materials were assimilated was extremely slow, long periods of incubation being necessary to insure appreciable utilization. Previous work had shown that the rate of growth, consumption of certain sugars, and fixation of nitrogen could be materially facilitated by drawing a current of air through the medium. It was hoped, by employing a similar method in these experiments, to shorten the time of incubation necessary to secure quantitative results of a definite character. Increased aeration unquestionably stimulated growth in many instances, but occasionally some difficulty was experienced in obtaining entirely satisfactory checking in quantitative nitrogen and volatile acid determinations following prolonged aeration, and in addition it was more difficult to maintain pure cultures. For these reasons the quantitative experiments in which *Azotobacter vinelandii* was employed were not aerated.

Utilization of formic acid.—Experiments were carried out in which formic acid was used as the sole organic constituent of the medium, but there was no indication of either growth, utilization of the acid, or fixation of nitrogen, and therefore the data are not recorded.

Utilization of acetic acid.—The data with regard to the utilization of acetic acid, recorded in table x, are quite conclusive in showing that the calcium salt of this acid is readily available to culture No. 62. Within seven days practically all the original 1.0 per cent of acid had disappeared, accompanied by abundant growth and a marked change in the reaction of the medium. In fact, it is probable that the hydroxyl-ion concentration was such as to inhibit further growth. Quite marked fixation of nitrogen was evident, but owing to an error in the method employed in the total nitrogen determinations in this experiment, the data are not recorded.

Utilization of propionic acid.—The ability of culture No. 62 to utilize readily the calcium salt of propionic acid is quite evident from the data presented in table xi. Within nine days practically all the acid had disappeared, and a marked increase in the hydroxyl-ion concentration and nitrogen content of the cultures had occurred.

TABLE X

UTILIZATION OF ACETIC ACID BY CULTURE NO 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	1059	——	Nitrogen fixation took place but owing to error in method the results were unsatisfactory.
2	Control 0	Sterile	7.0–7.4	1062	——	
3	2	Pure	7.0–7.4	831	229	
4	2	Pure	7.0–7.4	906	154	
5	4	(a)*	7.0–7.4	668	392	
6	4	(a)	7.0–7.4	654	406	
7	7	(a)	8.6–9.0	36	1024	
8	7	(a)	8.6–9.0	85	975	
9	9	Pure	9.0+	39	1021	
10	16	Contaminated	9.0+	48	1012	
11	16	Pure	9.0+	48	1012	
12	22	Contaminated	9.0+	124	936	
13	22	Pure	9.0+	91	969	

* Not tested.

TABLE XI

UTILIZATION OF PROPIONIC ACID BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	958	——	——	——
2	Control 0	Sterile	7.0–7.4	952	——	——	——
3	Control 18	Contaminated	8.2–8.6	17	——	——	——
4	Control 18	Sterile	7.0–7.4	974	——	——	——
5	3	Pure	7.0–7.4	829	132	1.72	76
6	5	Pure	7.0–7.4	705	256	4.74	54
7	7	Pure	7.0–7.4	626	335	3.64	92
8	9	——	9.0+	21	940	——	——
9	12	Pure	9.0+	37	924	4.74	196
10	18	Contaminated	9.0+	17	944	——	——

In this experiment control flasks Nos. 1 and 2 were not aerated, while Nos. 3 and 4 were aerated under the same conditions and for as long a time as any of the inoculated flasks. The culture adjacent to control culture No. 3 foamed badly, resulting in the contamination of No. 3 with *Azotobacter;* therefore it is not considered in the quantitative calculations. It is evident,

though, from a comparison of control flasks No. 1 and No. 2 with No. 4 that no volatilization of the propionic acid took place. Therefore the decrease in the quantity of propionic acid that occurred in the presence of pure cultures must have been due to its assimilation by the organisms.

Utilization of normal butyric acid.—The data presented in table XII show that culture No. 62 is also capable of utilizing normal butyric acid in its metabolism. Again only seven days were required for almost complete assimilation of the acid present, with corresponding decreases in the hydrogen-ion concentration. The quantities of nitrogen fixed were also marked, as was the visible growth of the organisms.

TABLE XII

UTILIZATION OF NORMAL BUTYRIC ACID AND FIXATION OF NITROGEN BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	978	—	—	—
2	Control 0	Sterile	7.0–7.4	995	—	—	—
3	2	Pure	7.0–7.4	956	30	.09	334
4	2	Pure	7.0–7.4	878	108	1.25	86
5	5	Pure	7.0–7.4	706	280	2.73	102
6	5	Pure	7.0–7.4	669	317	4.15	76
7	7	Pure	7.0–7.4	439	547	2.59	212
8	12	Pure	9.0+	78	908	6.77	134
9	17	Contaminated	9.0+	61	925	4.95	186
10	17	Contaminated	9.0+	111	875	6.29	140

Utilization of iso-butyric acid.—Under the experimental conditions to which the cultures recorded in table XIII were subjected there was little or no indication that culture No. 62 could utilize iso-butyric acid in its metabolism. It is true that there was some decrease in the quantity of volatile acid present in the different cultures but the quantities were small. Besides, the non-inoculated sterile aerated controls, No. 2 and No. 3, showed practically the same decrease as inoculated flask No. 10, incubated the same length of time. In addition there was no perceptible change in the reaction, and the quantities of nitrogen fixed, if any, did not exceed the experimental error. Visible growth was also

questionable. It seems safe, therefore, to conclude that culture No. 62 could not utilize the calcium salt of iso-butyric acid under the conditions obtaining in these experiments.

TABLE XIII

UTILIZATION OF ISO-BUTYRIC ACID BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	831	None	None
2	Control 17	Sterile	7.0–7.4	774	None	None
3	Control 17	Sterile	7.0–7.4	773	None	None
4	2	Pure	7.0–7.4	886	None	None
5	2	Pure	7.0–7.4	800	None	None
6	5	Contaminated	7.0–7.4	779	None	None
7	5	Pure	7.0–7.4	778	None	None
8	7	Contaminated	7.0–7.4	799	None	None
9	12	Pure	7.0–7.4	746	None	None
10	17	Contaminated	7.0–7.4	758	None	None

Utilization of normal valeric acid.—Not only was normal valeric acid not available to culture No. 62 but it actually was sufficiently toxic to kill all the introduced organisms within three days. This is the only instance in which any acid studied, other than formic, has actually killed the culture except when marked change in reaction occurred. There was of course no utilization of the acid or fixation of nitrogen. The slight loss of volatile acid previously referred to is evident in the data presented in table XIV.

Utilization of monohydrated valeric acid.[1]—The data presented in table XV with regard to this acid are inconclusive. There is a distinct loss of acid, evidently not due to its removal through aeration, because uninoculated aeration controls No. 3 and No. 4 incubated one day longer than the longest incubated inoculated flask showed no loss in volatile acid. On the other hand, there was no perceptible change in reaction, and the quantities of nitrogen fixed, if any, were too small to detect, there being no

[1] Mono- and trihydrated valeric acids were iso compounds made by Merck and Co.

TABLE XIV

UTILIZATION OF NORMAL VALERIC ACID BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed
1	Control 0	Sterile	6.6–7.0	992	None	None
2	Control 0	Sterile	6.6–7.0	992	None	None
3	3	Sterile	6.6–7.0	988	None	None
4	6	Contaminated	6.6–7.0	890	None	None
5	11	Sterile	6.6–7.0	990	None	None
6	11	Sterile	6.6–7.0	913	None	None
7	18	Sterile	6.6–7.0	973	None	None
8	18	Sterile	6.6–7.0	979	None	None
9	32	Sterile	6.6–7.0	935	None	None
10	32	Sterile	6.6–7.0	951	None	None

TABLE XV

UTILIZATION OF MONOHYDRATED VALERIC ACID BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	1055	—	None
2	Control 0	Sterile	7.0–7.4	1058	—	None
3	Control 33	Sterile	7.0–7.4	1064	—	None
4	Control 33	Sterile	7.0–7.4	1066	—	None
5	3	Pure	7.0–7.4	1051	10	None
6	6	Pure	7.0–7.4	944	117	None
7	11	Pure	7.0–7.4	911	150	None
8	11	Pure	7.0–7.4	972	89	None
9	18	Pure	7.0–7.4	899	162	None
10	18	Pure	7.0–7.4	907	154	None
11	32	Pure	7.0–7.4	871	190	None
12	32	Pure	7.0–7.4	933	128	None

difference in the nitrogen content of flasks No. 11 and No. 12 and sterile controls No. 3 and No. 4.

Utilization of trihydrated valeric acid.—Here again the quantities of volatile acid not recovered and increases in total nitrogen were not sufficient to be regarded as significant. If the quantities of acid disappearing are based upon aerated control No. 3 no losses are evident. Unfortunately, this sample became con-

taminated, and conclusions based upon it would not be entirely valid. On the other hand, if the quantities of acid recovered from the various flasks are compared with those recovered from controls No. 1 and No. 2, analyzed at the beginning of the experiment, small losses of acid are evident. What has been said with regard to losses of acid is equally true of increases in nitrogen. It is preferred, therefore, to regard it merely as a questionable possibility that culture No. 62 assimilates this acid qualitatively. The quantitative utilization of this acid, as well as of the monohydrated sample, is certainly small, if it occurs at all, compared to that of some of the other acid studied.

TABLE XVI

UTILIZATION OF TRIHYDRATED VALERIC ACID BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	784	Utilization questionable	Fixation questionable
2	Control 0	Sterile	7.0–7.4	785		
3	Control 19	Contaminated	7.0–7.4	726		
4	3	Pure	7.0–7.4	719		
5	3	Pure	7.0–7.4	776		
6	7	Pure	7.0–7.4	756		
7	7	Contaminated	7.0–7.4	752		
8	13	Pure	7.0–7.4	766		
9	13	Pure	7.0–7.4	732		
10	19	Contaminated	7.0–7.4	743		
11	19	Contaminated	7.0–7.4	756		

Utilization of normal caproic acid.—The data presented in table XVII show beyond question that the calcium salt of normal caproic acid may serve as a readily available source of organic material for culture No. 62. The samples analyzed after seven days' incubation, while still containing large quantities of volatile acid, showed marked changes in reaction, appreciable losses of acid, and fixation of nitrogen. The samples analyzed after thirteen days still contained appreciable quantities of acid but the hydroxyl-ion concentration had probably reached a point where growth was inhibited. This is further indicated by the failure to detect further losses of acid in the flasks incubated for a longer time, No. 10 and No. 11.

TABLE XVII

UTILIZATION OF NORMAL CAPROIC ACID BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	408	—	—	—
2	Control 19	Contaminated	9.0+	137	—	—	—
3	Control 19	Contaminated	7.0–7.4	359	—	—	—
4	3	Pure	6.6–7.0	351	57	1.02	56
5	3	Pure	7.0–7.4	374	34	.98	34
6	7	Pure	7.6–8.0	337	71	.50	142
7	7	Contaminated	7.8–8.2	260	148	2.16	69
8	13	Contaminated	9.0+	87	321	2.96	104
9	13	Contaminated	9.0+	75	333	Lost	—
10	19	Pure	9.0+	102	306	4.80	64
11	19	Pure	9.0+	109	299	—	—

Utilization of iso-caproic acid.—While the data presented in table XVIII may be regarded as inconclusive, they nevertheless indicate that iso-caproic acid is not available as an organic food for culture No. 62. There were slight losses of acid, but such losses were equally as marked from the non-inoculated, sterile, aerated controls as from any inoculated cultures. Further-

TABLE XVIII

UTILIZATION OF ISO-CAPROIC ACID BY CULTURE NO. 62

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed
1	Control 0	Sterile	7.0–7.4	560	Utilization questionable	Fixation questionable
2	Control 0	Sterile	7.0–7.4	533		
3	Control 19	Sterile	7.0–7.4	520		
4	Control 19	Sterile	7.0–7.4	497		
5	3	Pure	7.0–7.4	526		
6	3	Pure	7.0–7.4	—		
7	7	Pure	7.0–7.4	522		
8	7	Pure	7.0–7.4	505		
9	13	Pure	7.0–7.4	517		
10	13	Contaminated	7.0–7.4	493		
11	19	?	7.0–7.4	513		
12	19	Sterile	7.0–7.4	518		

more, there was no appreciable changes in reaction or detectable increases in the nitrogen content.

Summary of experiments with culture No. 62.—Under the experimental conditions to which culture No. 62 was subjected in the experiments herein reported the calcium salts of formic and normal valeric acids were strongly germicidal. Similar salts of acetic, propionic, normal butyric, and normal caproic acids served as readily available sources of organic food. The other salts tested, namely, iso-butyric, mono- and trihydrated valeric and iso-caproic, were either not available or utilized very slowly and in small quantities.

Experiments with Azotobacter vinelandii

The culture of *Azotobacter vinelandii* used in these experiments (Culture No. 94) was obtained from N. R. Smith, of the Bureau of Plant Industry, U. S. Department of Agriculture. It grew vigorously upon soil-extract-mannitol agar, less vigorously upon beef-extract agar, and produced the typical green fluorescence upon the former medium. It also grew very abundantly in the liquid medium employed when dextrose, mannitol, and calcium salts of several of the fatty acids were supplied as the organic material.

Utilization of formic acid.—There was no evidence either in the qualitative or quantitative experiments of the ability of this organism to utilize calcium formate and therefore the quantitative data are omitted.

Utilization of acetic acid.—An examination of the data presented in table XIX should convince any one of the ability of this culture to utilize readily the calcium salt of acetic acid. A very marked change in the reaction, an almost complete disappearance of the acid accompanied by definite fixation of nitrogen, together with an abundance of visible growth, substantiate the above conclusions. In this experiment the hydroxyl-ion concentration evidently reached a point that could not be tolerated by the organisms, most of them being dead when the flasks incubated for the longer period of time were examined.

Utilization of propionic acid.—*Azotobacter vinelandii* can readily assimilate propionic acid under the conditions obtaining in the

TABLE XIX

UTILIZATION OF ACETIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	876	—	—	—
2	Control	Sterile	7.0–7.4	859	—	—	—
3	4	Pure	7.0–7.4	783	84	−.06	—
4	4	Pure	7.0–7.4	790	77	.20	384
5	9	Pure	7.0–7.4	667	200	−.20	—
6	9	Pure	7.0–7.4	575	292	.12	440
7	14	Pure	7.0–7.4	423	444	.50	888
8	14	Pure	7.0–7.4	389	478	.96	498
9	24	Pure*	9.0+	3	864	1.60	540
10	24	Pure*	9.0+	3	864	3.06	282
11	33	Sterile	9.0+	5	862	2.36	366
12	33	Pure*	9.0+	11	856	2.22	386

* Very few living organisms.

experiment reported in table xx. Within three weeks the original 1.0 per cent of acid had practically disappeared. The abundance of visible growth, the marked increase in hydroxyl-ion concentration, and definite increases in the nitrogen content of the cultures are additional proof of the ability of the organism to assimilate this particular acid.

TABLE XX

UTILIZATION OF PROPIONIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	1009	—	—	—
2	Control	Sterile	7.0–7.4	999	—	—	—
3	7	Pure	7.0–7.4	790	214	.32	668
4	14	Pure	7.0–7.4	575	429	1.46	194
5	23	Pure	9.0+	16	988	5.92	168
6	23	Pure	9.0+	45	959	6.06	158
7	30	Pure	9.0+	7	997	4.46	224
8	30	Sterile	9.0+	10	994	4.02	247
9	39	Sterile	9.0+	7	997	3.12	319
10	39	Sterile	9.0+	7	997	2.36	422
11	46	Sterile	9.0+	4	1000	2.22	450
12	46	Sterile	9.0+	6	998	3.12	319

Utilization of normal butyric acid.—Some irregularities were exhibited in the growth in different culture flasks containing

normal butyric acid and inoculated with *Azotobacter vinelandii* despite all efforts to make the duplicate flasks as nearly identical as possible. These irregularities are reflected in the quantity of acid unrecoverable, the changes in reaction, and in the increases in nitrogen content as recorded in table XXI. However, these data unquestionably show a ready utilization of this acid by the culture in question. The rapidity of disappearance of the acid is not as great as with acetic and propionic acids, but the increases in nitrogen per unit of acid assimilated are greater.

TABLE XXI

UTILIZATION OF NORMAL BUTYRIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	806	—	—	—
2	Control	Sterile	7.0–7.4	819	—	—	—
3	9	Pure	7.0–7.4	761	51	.12	424
4	9	Pure	7.0–7.4	750	62	.38	162
5	16	Pure	7.0–7.4	700	112	.76	148
6	16	Pure	7.0–7.4	700	112	.64	176
7	25	Pure	7.0–7.4	499	313	2.62	118
8	25	Pure	7.0–7.4	314	498	5.80	90
9	39	Sterile	9.0+	46	766	6.12	126
10	39	Pure	8.4–8.8	321	491	3.82	128
11	53	Pure	9.0+	51	761	6.12	124
12	53	Pure	8.8–9.2	411	401	3.56	112

Utilization of iso-butyric acid.—The data presented in table XXII indicate rather strongly that the calcium salt of iso-butyric acid is not nearly so readily available as is the corresponding salt of the normal acid. Even after forty-nine days over half of the original acid was still present, the reaction had changed only slightly, and the quantity of nitrogen fixed was small compared with that fixed where the normal acid was present. Besides, the visible growth (unmistakably present) was also small compared to that where acetic, propionic, or normal butyric acid was the source of organic food.

Utilization of normal valeric acid.—This acid apparently was not assimilated by *Azotobacter vinelandii* as readily as some of the lower members of the series. However, the figures presented in table XXIII show practically complete disappearance in flasks

TABLE XXII

UTILIZATION OF ISO-BUTYRIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	835	—	—	—
2	Control	Sterile	7.0–7.4	846	—	—	—
3	7	Pure	7.0–7.4	795	45	Lost	—
4	7	Pure	7.0–7.4	790	50	Lost	—
5	14	Pure	7.0–7.4	753	87	.26	334
6	14	Pure	7.0–7.4	Lost	—	.32	—
7	17	Pure	7.0–7.4	700	140	.12	—
8	17	Pure	7.0–7.4	728	112	.64	174
9	26	Pure	7.0–7.4	662	178	.64	278
10	26	Pure	7.0–7.4	634	206	.64	322
11	38	Pure	7.0–7.4	495	343	1.22	282
12	49	Pure	7.0–7.4	467	373	1.14	338

Nos. 9, 11, and 12. The more rapid assimilation in these instances, though, might have been partially due to the contaminating organisms. That there was, however, unmistakable utilization in the uncontaminated flasks, Nos. 7, 8, and 10, is proved by the decreased acid content, change in reaction, and increase in nitrogen content. Both the total quantity of nitrogen fixed and the relative quantity fixed per unit of acid assimilated were large, the latter being greater than for any lower member of the fatty acid series.

TABLE XXIII

UTILIZATION OF NORMAL VALERIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	892	—	—	—
2	Control	Sterile	7.0–7.4	883	—	—	—
3	7	Pure	7.0–7.4	810	77	.70	110
4	7	Pure	7.0–7.4	835	52	.70	74
5	14	Contaminated	7.0–7.4	770	117	.96	122
6	14	Contaminated	7.0–7.4	750	137	1.34	102
7	26	Pure	8.8–9.2	197	690	6.68	102
8	26	Pure	8.8–9.2	621	266	2.80	96
9	38	Contaminated	9.0+	54	833	6.76	122
10	38	Pure	7.4–7.8	414	473	6.56	72
11	49	Contaminated	9.0+	62	825	7.65	108
12	49	Contaminated	9.0+	60	827	11.98	70

Utilization of monohydrated valeric acid.—Growth in the presence of this acid was slow, and the total amount appeared to be much less than with the normal valeric or with the acids of smaller molecular weight. This was reflected in the rate and total disappearance of the acid as well as in the quantity of nitrogen fixed. It is also evident from the data recorded in table XXIV that slight, if any, change took place in the hydrogen-ion concentration. However, the amount of nitrogen fixed and acid consumed, coupled with the presence of visible growth, show conclusively that this acid can be assimilated by the culture in question, but probably not as readily as the other low molecular weight straight-chain, fatty acids, at least not under the conditions of these experiments.

TABLE XXIV

UTILIZATION OF MONOHYDRATED VALERIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	989	—	—	—
2	Control	Sterile	7.0–7.4	1021	—	—	—
3	9	Pure	7.0–7.4	831	192	.64	300
4	9	Pure	7.0–7.4	830	175	.76	230
5	21	Pure	7.0–7.4	816	189	1.40	136
6	21	Pure	7.0–7.4	841	164	1.52	108
7	28	Pure	7.0–7.4	685	320	2.62	122
8	28	Pure	7.0–7.4	714	291	1.52	192
9	38	Pure	7.0–7.4	637	368	2.04	180
10	38	Pure	7.0–7.4	712	293	1.66	176
11	49	Pure	7.0–7.4	631	374	1.90	196
12	49	Pure	7.0–7.4	663	342	2.16	158

Utilization of trihydrated valeric acid.—What was said with regard to the monohydrated valeric acid also applies to the trihydrated, except that the quantities of acid assimilated and the quantities of nitrogen fixed were smaller. No perceptible change took place in the hydrogen-ion concentration, and only one-fifth of the acid was not recoverable after seven weeks of incubation. These facts would indicate that this acid is assimilable by *Azotobacter vinelandii* with somewhat more difficulty than either the normal or monohydrated valeric acids. The data are presented in table XXV.

TABLE XXV

UTILIZATION OF TRIHYDRATED VALERIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	784	—	—	—
2	Control	Sterile	7.0–7.4	788	—	—	—
3	7	Pure	7.0–7.4	730	56	.38	148
4	7	Pure	7.0–7.4	753	33	.26	122
5	14	Pure	7.0–7.4	729	57	.26	218
6	14	Contaminated	7.0–7.4	714	72	.32	224
7	24	Pure	7.0–7.4	752	34	.50	68
8	24	Pure	7.0–7.4	708	78	.88	88
9	35	Pure	7.0–7.4	656	130	1.28	116
10	35	Pure	7.0–7.4	668	118	1.22	96
11	49	Contaminated	7.0–7.4	632	154	.76	202
12	49	Pure	7.0–7.4	628	158	.64	246

Utilization of normal caproic acid.—It would appear from the information recorded in table XXVI that normal caproic acid can be metabolized by *Azotobacter vinelandii* the most readily of any fatty acid tested. Within four days a very heavy growth was evident, half the acid added to the medium had disappeared, the reaction had become alkaline to thymol-blue, and marked fixation of nitrogen had taken place. Within nine days the volatile acid had reached the minimum recorded for any incubation period. Furthermore, the quantity of nitrogen fixed per

TABLE XXVI

UTILIZATION OF NORMAL CAPROIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as P_H	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	408	—	—	—
2	Control	Sterile	7.0–7.4	381	—	—	—
3	4	Pure	9.0+	267	128	3.92	32
4	4	Pure	9.0+	180	215	4.66	46
5	9	?	9.0+	39	356	5.86	60
6	9	Pure	9.0+	41	354	5.48	64
7	16	Pure	9.0+	32	363	6.06	60
8	16	Pure	9.0+	28	367	6.62	56
9	28	Contaminated	9.0+	27	368	5.28	70
10	28	Contaminated	9.0+	31	364	6.50	56
11	37	Contaminated	9.0+	35	360	8.34	82
12	37	Pure	9.0+	35	360	5.10	70

unit of acid assimilated was greater than for any other acid tested quantitatively. This would seem to indicate that increasing the size of the molecule does not necessarily decrease its availability.

Utilization of iso-caproic acid.—This acid was, according to the data presented in table XXVII, readily assimilated, though the rate of growth, acid utilization, and nitrogen fixation were not equal to the corresponding rates where normal caproic acid was the sole organic food supplied. Similarly, the ratio between acid consumed and nitrogen fixed was twice as wide as for the normal acid. The iso compound then, it would seem, is not only less readily metabolized but can also not be used as economically as the straight-chain molecule of this acid.

TABLE XXVII

UTILIZATION OF ISO-CAPROIC ACID AND FIXATION OF NITROGEN BY AZOTOBACTER VINELANDII

Flask No.	Days incubated	Purity	Approximate reaction expressed as Ph	Mgs. acid recovered	Mgs. acid utilized	Mgs. nitrogen fixed	Mgs. acid used per mg. nitrogen fixed
1	Control	Sterile	7.0–7.4	417	—	—	—
2	Control	Sterile	7.0–7.4	409	—	—	—
3	7	Pure	7.8–8.2	323	90	.50	180
4	7	Pure	7.8–8.2	272	131	.90	144
5	16	Pure	8.2–8.6	90	323	2.28	142
6	16	Pure	8.2–8.6	75	358	2.16	156
7	28	Pure	9.0+	23	390	2.54	154
8	28	Pure	9.0+	22	391	3.18	122
9	37	Pure	9.0+	77	336	3.70	90
10	37	Pure	9.0+	23	390	2.80	140
11	51	Sterile	9.0+	17	396	2.54	156
12	51	Pure*	9.0+	15	398	2.68	148

* Only four colonies developed on two plates.

Summary of experiments with Azotobacter vinelandii (culture No. 94).—*Azotobacter vinelandii* is capable of growing in a medium containing as the only organic material the calcium salt of the following fatty acids: acetic, propionic, normal butyric, isobutyric, normal valeric, iso-valeric (monohydrated valeric and trihydrated valeric), normal caproic, and iso-caproic. This organism failed to grow under similar conditions in the presence of calcium formate.

The rate of growth varies with the different calcium salt added

to the medium, being very rapid with normal caproic and very slow with all of the iso acids tested. When growth takes place there is an increase in the nitrogen content of the medium and a decrease in the quantity of volatile acid.

The quantity of nitrogen fixed in the presence of any given acid corresponds more or less closely with the quantity of acid disappearing. The increase in nitrogen per unit of acid consumed by the organisms varies with different acids. If only normal acids are considered the quantity of nitrogen fixed per unit of acid decomposed increases as the molecular weight of the acid increases. Growth, disappearance of acid, and increase in nitrogen are not as rapid where iso acids are added to the medium as when the acid is a normal compound.

Experiments with Other Cultures

Since there were a number of instances in which the results secured with cultures No. 62 and No. 94 did not agree, it seemed desirable to extend somewhat similar tests to other cultures. In order to secure very active nitrogen-fixing strains for these tests the experiment recorded in table xxviii was arranged. It was also hoped that this experiment would show to what extent vigorous growth in liquid media, utilization of dextrose, and fixation of nitrogen could be correlated.

Erlenmeyer flasks of 300 cc. capacity containing 1.0 per cent dextrose medium were prepared and inoculated heavily with the cultures indicated. One of the triplicate flasks was used for qualitative sugar tests. Growth observations were recorded from the remaining two flasks and after fifteen days' incubation the quantity of nitrogen fixed was determined.

Since the dextrose had completely disappeared in all but two instances and the original quantities in the various cultures were identical, the total nitrogen figures represent approximately the quantity of nitrogen fixed per 1000 mgs. dextrose consumed. It will be noted that with few exceptions the quantities of nitrogen fixed do not vary very widely. The smallest quantity fixed in any instance where complete disappearance of sugar had taken place was 2.64 mgs. while the largest was 11.46 mgs. Most of the cultures showed a fixation of about 8 to 10 mgs. per 1000

TABLE XXVIII

THE ABILITY OF VARIOUS AZOTOBACTER CULTURES TO GROW IN THE PRESENCE OF, AND TO ASSIMILATE, DEXTROSE, AND THEIR RELATIVE ABILITY TO FIX NITROGEN

Culture No.	Quantity of growth after varying periods of incubation			Presence of dextrose after varying periods of incubation		Nitrogen fixed per 100 cc. medium
	2 days	4 days	8 days	8 days	14 days	Mgs.
219	?	?	+	Abundant	0	8.14
187(a)	+	++++	++++	0	0	10.14
55	0	0	++	Abundant	0	9.16
209	++	++++	++++	0	0	9.92
C	++	+++	+++	0	0	10.62
94	+++	++++	++++	0	0	8.00
204	?	+++	++++	0	0	9.16
220	?	+	++	Abundant	0	9.10
15	?	?	?	Abundant	Abundant	2.64
19	+++	++++	++++	0	0	10.00
209	+	+++	++++	0	0	9.54
27	?	?	+	0	0	10.06
215(4)	++	+++	+++	0	0	8.66
II	++	+++	+++	Abundant	0	10.06
216	+++	+++	++++	0	0	9.04
144	?	?	++	0	0	10.38
16	?	?	++	Abundant	Abundant	2.74
103(4)	?	++++	++++	0	0	8.92
226(B)	+	+	++++	0	0	7.04
188	++++	++++	++++	0	0	8.28
86	+++	++++	++++	0	0	11.46
97	+++	+++	++++	0	0	9.30
95	++	+++	+++	0	0	7.06
B	?	?	+	Abundant	0	10.70
7	?	+	++	0	0	7.96
48	?	+	+++	Abundant	0	10.32
11(2)	++	+++	+++	0	0	8.92
56	?	+	++	0	0	9.16
S-2	0	?	+	Abundant	0	6.88
194	0	+	++	0	0	9.80
185	+	+	+++	0	0	8.08
165	?	+	++++	0	0	10.06
25	?	+++	+++	0	0	8.94
44	0	0	+	Abundant	0	8.46
I	0	+	+++	0	0	8.66
218	?	+++	+++	0	0	8.84
III	+	+++	+++	0	0	6.56
215(2)	+	+++	+++	0	0	6.24
178	0	?	++	0	0	10.62
198(1)	+	+++	+++	0	0	8.78
15(1)	0	0	+	0	0	7.64
Control	0	0	0	Abundant	Abundant	——
Control	0	0	0	Abundant	Abundant	——
Control	0	0	0	Abundant	Abundant	——

mgs. of dextrose or 100 to 120 parts of sugar consumed for each part of nitrogen fixed. This would indicate that the organic

food available, provided the particular culture in question is capable of utilizing it, is possibly of more significance in determining the quantity of nitrogen fixed than is the culture. There was, however, a rather marked variation in the rate at which various cultures consumed the dextrose.

Another very evident fact is that the quantity of visible growth cannot be taken as necessarily indicating the relative fixation of nitrogen. Cultures Nos. 219, 55, 220, 27, 144, B, 44, and 178 all showed a relatively small visible growth, yet they were among the most active nitrogen-fixing strains. Cultures Nos. 15 and 16 were evidently unable to utilize dextrose very readily. It is possible, though, that they may have fixed as much nitrogen per unit of dextrose consumed as any other culture.

From the cultures tested in the experiment just described nine, Nos. 7, C, 165, II, 188, 194, 187, 178, 218, and in addition R, were chosen for a comparative study of their ability to utilize the various acids studied in previous experiments. These particular cultures were selected both because of their active nitrogen-fixing ability and because they were secured from such widely varying conditions. Furthermore, they exhibited rather marked variations in cultural characteristics, indicating that they represented different strains or possibly species. In this experiment 100 cc. of the medium were placed in 750-cc. or 1000-cc. flasks, thus giving excellent aeration.

The rate of visible growth is indicated in table xxix, while the quantities of acid consumed and nitrogen fixed are recorded in table xxx.

The data presented in tables xxix and xxx tend to confirm the previous results secured from cultures No. 62 and 94 in that rather marked variations are exhibited in the ability of various cultures to grow in the presence of calcium salts of different organic acids as the only organic matter present.

All ten of the cultures readily assimilated dextrose, though culture No. II probably with somewhat more difficulty than the others. All grew in the presence of the calcium salts of acetic, propionic, normal valeric, normal butyric and normal caproic acids, the latter apparently being more easily metabolized than

TABLE XXIX

RELATIVE ABILITY OF TEN DIFFERENT CULTURES OF AZOTOBACTER TO GROW WHERE THE CALCIUM SALT OF DIFFERENT FATTY ACIDS WAS THE ONLY SOURCE OF ORGANIC FOOD

Culture No.	Growth in the presence of									
	Acetic acid	Propionic acid	Normal butyric acid	Iso-butyric acid	Normal valeric acid	Mono-hydrated valeric acid	Tri-hydrated valeric acid	Normal caproic acid	Iso-caproic acid	Dextrose
R (a)*	+++	++	0	?	++++	+	0	++++	0	++++
(b)	+++	+++	0	?	++++	+	0	++++	0	++++
(c)	+++	+++	0	?	++++	++	+	++++	0	++++
(d)	++++	+++	+	?	++++	++	+	++++	0	++++
(e)	++++	+++	+	?	++++	++	+	++++	0	++++
7 (a)	++	+	?	0	?	0	0	++	0	+++
(b)	++	+	+	?	?	0	0	++	0	+++
(c)	++	++	+	?	+	0	0	++++	0	+++
(d)	+++	+++	+	?	+++	0	0	++++	0	+++
(e)	++++	+++	+	+	+++	?	+	++++	0	+++
C (a)	+	+	0	?	+	?	?	+++	0	+++
(b)	+	+	?	?	+	?	?	+++	0	+++
(c)	+	+	+	?	++	?	?	+++	0	+++
(d)	+	++	++	?	+++	?	?	+++	0	+++
(e)	+++	++	+++	?	+++	?	?	+++	0	+++
218 (a)	++	+	0	0	++	+	0	++++	0	++++
(b)	+++	++	0	0	+++	+	?	++++	0	++++
(c)	+++	+++	+	+	++++	+	+	++++	0	++++
(d)	+++	+++	++	+	++++	+	++	++++	0	++++
(e)	++++	+++	++	+	++++	+	++	++++	0	++++
165 (a)	+	++	?	0	+	?	0	+	0	++++
(b)	+	+++	++	?	++	?	?	+	0	++++
(c)	+	+++	++	?	+++	+	?	++	0	++++
(d)	++	+++	++	+	+++	+	+	+++	0	++++
(e)	++	++++	++++	+	++++	+	+	+++	0	++++

TABLE XXIX (*continued*)

Culture No.	Growth in the presence of									
	Acetic acid	Propionic acid	Normal butyric acid	Iso-butyric acid	Normal valeric acid	Mono-hydrated valeric acid	Tri-hydrated valeric acid	Normal caproic acid	Iso-caproic acid	Dextrose
II (a)	?	0	0	0	?	?	0	+	0	?
(b)	+	0	0	0	?	?	0	+	0	+
(c)	+	?	0	0	+	?	0	+	0	+++
(d)	+	+	?	0	+	?	0	+	0	+++
(e)	++	++	+	?	+	?	0	+	0	+++
188 (a)	+++	+	+	+	+++	++	+	++	0	++++
(b)	+++	+	+	+	+++	++	+	+++	0	++++
(c)	+++	+	+	+	+++	++	++	+++	0	++++
(d)	+++	++	++	++	++++	++	++	+++	0	++++
(e)	++++	+++	++++	++	++++	++	++	+++	0	++++
194 (a)	+	+	?	0	++	0	0	+++	0	++++
(b)	+	+	?	?	++++	+	0	+++	0	++++
(c)	++	+	?	?	++++	+	0	+++	0	++++
(d)	+++	++	+	?	++++	+	0	+++	0	++++
(e)	++++	++	++	+	++++	+	?	++++	0	++++
187 (a)	+	+	?	+	+	?	?	+++	0	+++
(b)	+	+	+	+	++	?	?	+++	0	++++
(c)	+	+	+	+	+++	?	?	+++	0	++++
(d)	+	+	+	+	+++	+	?	+++	0	++++
(e)	+++	+	+++	+	+++	+	?	+++	0	++++
178 (a)	+	+	+	+	++	+	?	+++	0	+++
(b)	+	+	+	+	+++	+	?	++++	0	++++
(c)	+	+	+	+	++++	+	?	++++	0	++++
(d)	++	+	+	+	++++	+	?	++++	0	++++
(e)	++	++	+	+	++++	++	?	++++	0	++++

* (a) Observations made after 5 days incubation at 30° C.
(b) Observations made after 8 days incubation at 30° C.
(c) Observations made after 13 days incubation at 30° C.
(d) Observations made after 23 days incubation at 30° C.
(e) Observations made after 25 days incubation at 30° C.

TABLE XXX

GROWTH, UTILIZATION OF VARIOUS FATTY ACIDS, AND NITROGEN FIXED BY TEN DIFFERENT CULTURES OF AZOTOBACTER

Culture No.	Acetic acid	Propionic acid	Normal butyric acid	Iso-butyric acid	Normal valeric acid	Mono-hydrated valeric acid	Tri-hydrated valeric acid	Normal caproic acid	Iso-caproic acid	Dextrose
Visible growth (35 days incubation)										
R	++++	+++	+	?	++++	++	+	++++	0	++++
7	+++	++++	++	+	+++	?	+	++++	0	+++
C	+++	++	+++	?	+++	?	?	+++	0	+++
218	++++	+++	++	+	++++	+	++	++++	0	++++
165	++	++++	++++	+	++++	+	?	++++	0	++++
II	++	++	+	?	+	?	0	+	0	+++
188	+++	+++	++++	++	++++	++	++	+++	0	++++
194	++++	++	++	+	++++	+	?	++++	0	++++
187	+++	+	+++	+	+++	+	?	+++	0	++++
178	++	++	+	+	++++	++	?	++++	0	++++
Mgs. acid consumed										
R	883	618	276	71	378	152	—33	393	7	818
7	884	646	300	101	374	165	16	362	15	818
C	892	372	375	131	361	84	16	287	1	818
218	896	652	268	142	382	176	143	360	28	818
165	434	644	367	72	374	149	24	379	2	818
II	358	284	251	99	246	116	47	163	15	528
188	582	621	686	247	371	83	35	271	41	818
194	685	547	289	29	370	77	—51	247	1	818
187	385	386	189	247	375	143	7	393	21	818
178	379	391	308	70	365	57	—24	379	16	818

TABLE XXX (*continued*)

Culture No.	Acetic acid	Propionic acid	Normal butyric acid	Iso-butyric acid	Normal valeric acid	Mono-hydrated valeric acid	Tri-hydrated valeric acid	Normal caproic acid	Iso-caproic acid	Dextrose
					Mgs. nitrogen fixed					
R	3.19	2.29	2.29	.64	2.68	1.14	.26	3.06	.00	3.32
7	1.53	2.55	2.29	.77	3.82	1.02	.00	3.32	.00	4.72
C	2.68	1.53	2.04	.89	3.44	1.02	.77	4.08	.00	6.42
218	1.52	1.27	1.27	3.52	1.65	.77	1.14	3.82	.00	3.06
165	1.14	2.04	2.04	.51	2.55	.89	.12	3.44	.00	6.50
II	.77	1.02	1.02	.51	2.43	.64	.12	1.53	.00	5.10
188	1.53	3.32	3.82	.77	2.55	1.02	.00	4.08	.00	8.16
194	1.53	2.80	2.04	.64	1.53	1.27	.00	3.32	.00	6.42
187	1.40	1.40	1.32	.51	2.04	1.53	.00	3.82	.00	5.61
178	1.53	1.78	1.65	.77	1.78	.89	.00	3.95	.00	8.67
					Mgs. acid used per mg. nitrogen fixed					
R	277	270	121	109	141	133	—	128	—	247
7	578	253	131	131	98	162	—	109	—	173
C	333	243	135	147	115	82	—	70	—	127
218	585	513	211	—	231	229	—	95	—	267
165	381	315	180	141	147	167	—	111	—	126
II	463	278	246	194	101	181	—	107	—	103
188	367	187	179	321	143	81	—	66	—	100
194	448	231	141	—	241	61	—	74	—	127
187	275	276	143	484	184	93	—	103	—	164
178	248	220	187	91	205	77	—	96	—	94
Average	396	270	167	202	160	117	...	96	..	153
Mgs. nitrogen fixed per gm.	2.53	3.58	6.00	4.95	6.25	8.5		10.42		6.54
Mgs. nitrogen fixed per calory	.72	.72	1.01	.83	.93	1.27		1.45		1.73

any of the others, with valeric ranking next. It is quite evident, then, that increasing the size of the molecule does not decrease the availability. Not one of the cultures seemed capable of growing when the calcium salt of iso-caproic acid was the sole organic compound present. Growth with the calcium salts of iso-butyric or with the two hydrated valeric acids (the only organic materials present) was usually either very slow or absent. Culture No. 188 seemed to utilize a wider variety of acids with more ease than any other, its growth being recorded as + after three weeks with all the different acids except iso-caproic.

As previously pointed out, the quantity of visible growth is not necessarily associated with the quantity of nitrogen fixed or the quantity of organic material consumed. This is again evident if the visible growth as recorded in table XXIX is compared with the quantity of acid utilized and nitrogen fixed as recorded in table XXX.

The quantitative data presented in table XXX show very definitely that all ten of the strains of *Azotobacter* used in this experiment can utilize, as a source of organic food for nitrogen-fixing purposes, all the acids tested with the exception of trihydrated valeric and iso-caproic. Cultures C and 218 apparently utilized the trihydrated valeric acid. The iso compounds, though, cannot be assimilated as readily as the straight-chain molecules. Since this experiment could not be repeated no effort will be made to analyze critically the results secured with the individual cultures. It is quite evident that some of the cultures can assimilate certain acids very much more readily than can other cultures. Furthermore, some were capable of fixing very much more nitrogen per unit of acid with a given acid than were others.

The milligrams of acid consumed per milligram nitrogen fixed, the nitrogen fixed per gram acid, and the quantity of nitrogen fixed per calory of contained energy for the various acids were averaged and recorded at the end of table XXX. In a general way this summary agrees with the results secured with *Azotobacter vinelandii.* The quantity of nitrogen fixed per gram of acid metabolized increases as the molecular weight increases. In fact the increase in quantity of nitrogen fixed is more rapid

than the increase in heat of combustion, indicating a more efficient use of the energy contained in the larger molecules.

The conclusion seems justified, then, that the calcium salts of acetic, propionic, normal butyric, normal valeric, and normal caproic acids can be very readily assimilated by numerous strains of *Azotobacter*, while the ability to assimilate iso-caproic acid is rather limited among these organisms. The other acids tested, namely, iso-butyric and iso-valeric acids, while capable of being assimilated by most of the cultures tested, are certainly not as readily available as are acetic, propionic, normal valeric, and normal caproic.

As a further check on the relative availability of the various acids the protocol arranged in table XXXI was carried out experimentally. The acids used in this experiment were all from new lots and, because of limited quantities available, only approximately 0.5 per cent concentrations were used. Even with 0.5 per cent, large quantities of heptylic and caprylic acids remained undissolved in the culture medium. Erlenmeyer flasks of 300 cc. capacity containing 50 cc. of the medium and inoculated in duplicate served as cultures.

In addition to the fatty acids a number of polyhydric alcohols of varying molecular weights and some of identical molecular weights but varying configuration were used in order to see if similar variability in assimilability, as observed for acids, existed for alcohols.

Culture No. 94 again demonstrated its superiority over either No. 178 or No. 218 to utilize a variety of fatty acids, and also to metabolize more readily the alcohols. Both the latter cultures again failed to utilize any of the iso compounds readily and some not at all. These data, secured from entirely different batches of acids, tend to substantiate the observations noted from experiments recorded earlier in this paper. One new acid, di-methyl-ethyl-acetic, was added but apparently was not even assimilated by culture No. 94.

The same variability as regards the utilization of different acids by different strains of *Azotobacter* is also evident when the alcohols are considered. Of the eight polyhydric alcohols tested, only sorbitol and mannitol were readily metabolized by

TABLE XXXI

QUALITATIVE TESTS OF THE ABILITY OF AZOTOBACTER CULTURES NOS. 94, 178, AND 218 TO UTILIZE VARIOUS ORGANIC ACIDS AND ALCOHOLS

Organic material	Culture No. 94				Culture No. 178				Culture No. 218			
	6 days	10 days	19 days	39 days	6 days	10 days	19 days	39 days	6 days	10 days	19 days	39 days
Formic acid	0	0	0	0	0	0	0	?	0	0	0	0
Acetic acid	+++	+++	+++	+++	++	+++	+++	+++	+	++	++	+++
Propionic acid	+++	+++	+++	+++	++	+++	+++	+++	++	+++	+++	+++
Lactic acid	+++	+++	+++	+++	++	+++	+++	+++	+++	+++	+++	+++
Normal butyric acid	+++	+++	+++	+++	+	+	+++	+++	+++	+++	+++	+++
Iso-butyric acid	++	++	+++	+++	?	?	?	+	?	+	+	++
Normal valeric acid	+++	+++	+++	+++	+	+	+++	+++	++	+++	+++	+++
Iso-valeric acid	0	+	++	+++	0	0	0	?	0	?	+	++
Normal caproic acid	+++	+++	+++	+++	+	++	++	+++	++	+++	+++	+++
Iso-caproic acid	+	+	+++	+++	?	?	?	?	0	0	0	?
Normal heptylic acid	+++	+++	+++	+++	?	+	++	+++	0	++	++	+++
Normal caprylic acid	+++	+++	+++	+++	?	?	?	+++	0	?	?	++
Di-methyl-ethyl-acetic acid	0	0	0	0	0	0	0	0	0	0	0	0
Ethylene glycol	0	0	0	+	0	0	0	0	0	0	0	0
Glycerol	+	++	++	+++	0	0	0	0	0	0	+	+++
Adonitol	0	0	0	+	0	0	0	0	0	0	0	0
Mannitol	+++	+++	+++	+++	0	+	+++	+++	0	0	++	+++
Dulcitol	0	0	0	+	0	0	0	0	0	0	0	0
Erythritol	+++	+++	+++	+++	0	0	0	0	0	0	0	0
Inositol	+++	+++	+++	+++	0	0	0	0	0	0	?	++
Sorbitol	+++	+++	+++	+++	+	++	+++	+++	0	++	+++	+++
Control	0	0	0	+	0	0	0	0	0	0	0	0
Control	0	0	0	+	0	0	0	0	0	0	0	0

all three cultures, the former more rapidly than the latter. Dulcitol, an isomer of sorbitol and mannitol, apparently cannot be utilized by any of the three cultures. Inositol, a six carbon hexahydric ring alcohol, was readily utilized by culture No. 94, with more difficulty by culture No. 218, and not at all by culture No. 178. The same was true of glycerol. The four carbon alcohol of this series, erythritol, was utilized only by culture No. 94. The two and five carbon numbers, ethylene glycol and adonitol, were apparently not available to any of the three cultures. This fact is rather interesting since Mockeridge obtained the maximum fixation in her experiments where ethylene glycol was the sole source of energy. Apparently the configuration of the molecule plays an important role in determining the ability of a given strain of *Azotobacter* to utilize a compound.

Discussion

Attention has already been called to the salient facts brought out in the various experiments in the summaries accompanying the individual tables. In the limited discussion to follow an effort will be made merely to correlate these various points with the special object of trying to see if satisfactory answers to the original questions propounded in the introduction can be made.

In the first place, it is frankly admitted that certain procedures followed in some of the earlier experiments did not prove as satisfactory as had been hoped. This was true of the aeration in that the quantitative acid and nitrogen data did not, for some unknown reason, check as well as did later experiments. Because of these irregularities as much significance is not attached to the data secured in connection with those experiments as to those in which culture No. 94 was employed.

Secondly, such variation in the ability of different cultures to utilize different organic food substances was not anticipated or the experiments would have been confined entirely to identified cultures, thereby making it possible to compare results here reported with results obtained by other investigators. This desirability was realized in time to make use of known cultures in the major portion of these experiments, and data obtained with known organisms are regarded as much more significant.

In the third place the inadequacy of the data, in many or possibly all instances, from a quantitative point of view, is realized. It is believed, however, that in this respect they are equal or superior to any thus far reported. Where quantitative determinations, such as were employed in these experiments, are necessary the accumulation of mass data is a slow process. The limited data available are presented not as definite proof but rather as indicating certain tendencies, and it is hoped that others may see fit to conduct experiments along similar lines, thus bringing about the accumulation of sufficient data to justify definite conclusions.

It is desired to call attention again to, and to emphasize, the danger of applying the findings from a study of one strain of *Azotobacter* to other strains. If there is any one thing indicated by the experiments reported in this paper it is the marked variability in the metabolism of organic compounds of different strains or species in this group of organisms. This fact makes it rather difficult to compare results that have been reported from one laboratory with those from another, because frequently no indication whatsoever has been given as to the origin or identification of the culture studied. In the future much greater emphasis should be placed upon the identity of the culture being studied. For the reason just set forth it is believed that very little would be gained by a comprehensive review of investigations dealing with the utilization of various organic substances by this group of organisms.

A cursory perusal of the literature dealing with *Azotobacter* will impress one with the great variety of organic compounds that may be assimilated by these organisms. Also it brings out the wide variation in efficiency with which such compounds can be used when the quantity of nitrogen fixed in their presence is the criterion by which such efficiency is judged.

To illustrate the points suggested in the preceding paragraph the reader is referred to table XXXII. This table is an adaptation of one recently used by Bonazzi ('26) enlarged to include the work of Mockeridge and a few examples from the data previously presented in this paper.

Over fifty separate and distinct organic compounds are here

TABLE XXXII

RELATIVE FIXATION OF NITROGEN PER GRAM ORGANIC FOOD OBSERVED BY DIFFERENT INVESTIGATORS

Organic compound in medium	Mgs. nitrogen fixed per gram organic material						
	Löhnis and Pillai—impure		Hoffmann and Hammer		Krainsky	Mockeridge	Gainey
	$+CaCO_3$	$-CaCO_3$	Impure	Pure	Pure	Pure	Pure*
Polysaccharides:							
Starch	3.36	3.50			0.40	5.93	
Dextrine	7.18	7.58	1.72	13.40	1.20	6.62	
Inulin	7.72	7.58	1.35	10.85	5.80	9.76	
Gums:							
Gum arabic						6.13	
Gum tragacanth						9.13	
Sugars:							
Raffinose			2.23	5.35	1.60		
Saccharose	8.60	5.90	0.93	11.70	0.00	7.28	
Maltose	7.44	7.86	0.74		2.80	7.55	
Lactose	9.12	8.88	4.64	7.20	0.80	3.39	
Levulose	8.52	8.80	1.68	10.30	5.55	10.32	
Galactose	7.86	7.44	1.16	7.35	0.67	6.20	
Dextrose	4.62	4.36	1.65	8.95	1.35	6.57	8.85
Xylose	9.54	9.40		4.55		9.00	
Mannose				7.90			
Arabinose	7.62	7.34		10.00	0.60	9.28	
Alcohols:							
Mannitol	9.40	9.96	4.33	14.40	5.70	11.62	
Erythritol					0.00	4.88	
Glycerol	4.78	1.68		5.05	2.40	5.00	
Ethylene glycol						16.74	
Methyl					0.00	2.10	
Ethyl					1.00	4.02	
Propyl						9.02	
Iso-butyl						4.69	

TABLE XXXII (*continued*)

Organic compound in medium	Mgs. nitrogen fixed per gram organic material						
	Löhnis and Pillai—impure		Hoffmann and Hammer		Krainsky	Mockeridge	Gainey
	$+CaCO_3$	$-CaCO_3$	Impure	Pure	Pure	Pure	Pure*
Salts of fatty acids:							
Ca-formate						1.47	0.00
Ca-acetate					3.20	3.77	2.60
Na-propionate	1.10	0.96					
Ca-propionate					0.00	5.16	5.66
Ca-butyrate	0.02	0.16				6.08	6.52
Ca-butyrate (iso)							3.53
Ca-valeriate (normal)							10.71
Ca-valeriate (monohydrated)							5.99
Ca-valeriate (trihydrated)							7.49
Ca-caproate							17.87
Ca-caproate (iso)							7.57
Salts of other organic acids:							
Na-succinate	2.96	2.82					
Ca-succinate						8.60	
Na-citrate	1.42	1.00			1.60	6.44	
Ca-lactate	2.49	2.22				12.01	
K-oxalate	0.12	0.26					
Na-tartrate	5.06	2.82					
Ca-tartrate						4.54	
Ca-racemate						2.77	
Ca-malonate						5.32	
Ca-mucate						6.79	
Ca-fumarate						2.00	
Ca-maleate						1.88	
Ca-glycollate						1.75	
Ca-malate						5.19	

* Data for dextrose secured with culture No. 62 (*Azotobacter chroococcum*). Data for Ca-formate from large number of cultures including *Azotobacter chroococcum* and *Azotobacter vinelandii*. Other data are for culture No. 94 (*Azotobacter vinelandii*).

recorded as being assimilable by *Azotobacter*. Among these are representatives of classes of organic compounds possessing, in many instances, very few characteristics in common. Furthermore, the compounds here listed are only those reported by five of the many investigators in this field and are by no means intended to represent all compounds that have been tested and found capable of supplying the organic needs of members of the *Azotobacter* group of organisms. Among the carbohydrates are examples of polysaccharides, gums, and sugars. Among the latter are tri-, di-, and mono-saccharoses as well as hexose and pentose sugars. Alcohols are represented by mono-, di-, tri-, tetra-, and hexa-hydrox compounds, also by straight-chain and iso arrangements of the carbons, with the additional variations in polarity of inactive, dextro-, and levo-rotary molecules. There are also twenty-five salts of organic acids, including representatives of a number of dissimilar groups. There would seem to be no question, then, but that among the species of *Azotobacter* there are members capable of utilizing a very wide variety of organic compounds as the only organic requirement for the fixation of nitrogen. Not only is this true but the same strain of organisms can function as a nitrogen fixer when supplied with a wide variety of compounds.

When it comes to the comparative efficiency with which these various compounds can be used, measured by quantitative gains in nitrogen, the data are too inadequate to permit of drawing any very definite conclusions. The work with impure cultures would have to be eliminated from consideration. This leaves only a few compounds that have been tested by two or more investigators. Of these ten may be selected that were studied in common by Hoffmann and Hammer ('10), Krainsky ('08), and Mockeridge ('15). The quantity of nitrogen fixed per gram of material as reported by these investigators is indicated in fig. 3.

The data plotted may not be very accurate, since there is no indication of quantitative determinations of the residual organic material having been made, except that Mockeridge states that qualitative tests showed complete absence of the organic compound. Furthermore, one is forced to assume that the original

1.0 per cent of material added remained quantitatively unaltered during the process of sterilization, a condition that certainly might not obtain in all cases. In this connection it is believed that the policy followed in experiments herein reported, of making quantitative determinations on controls submitted to the same treatment as the cultures, is a much safer procedure for ascertaining the quantity of the organic compound available to the organisms.

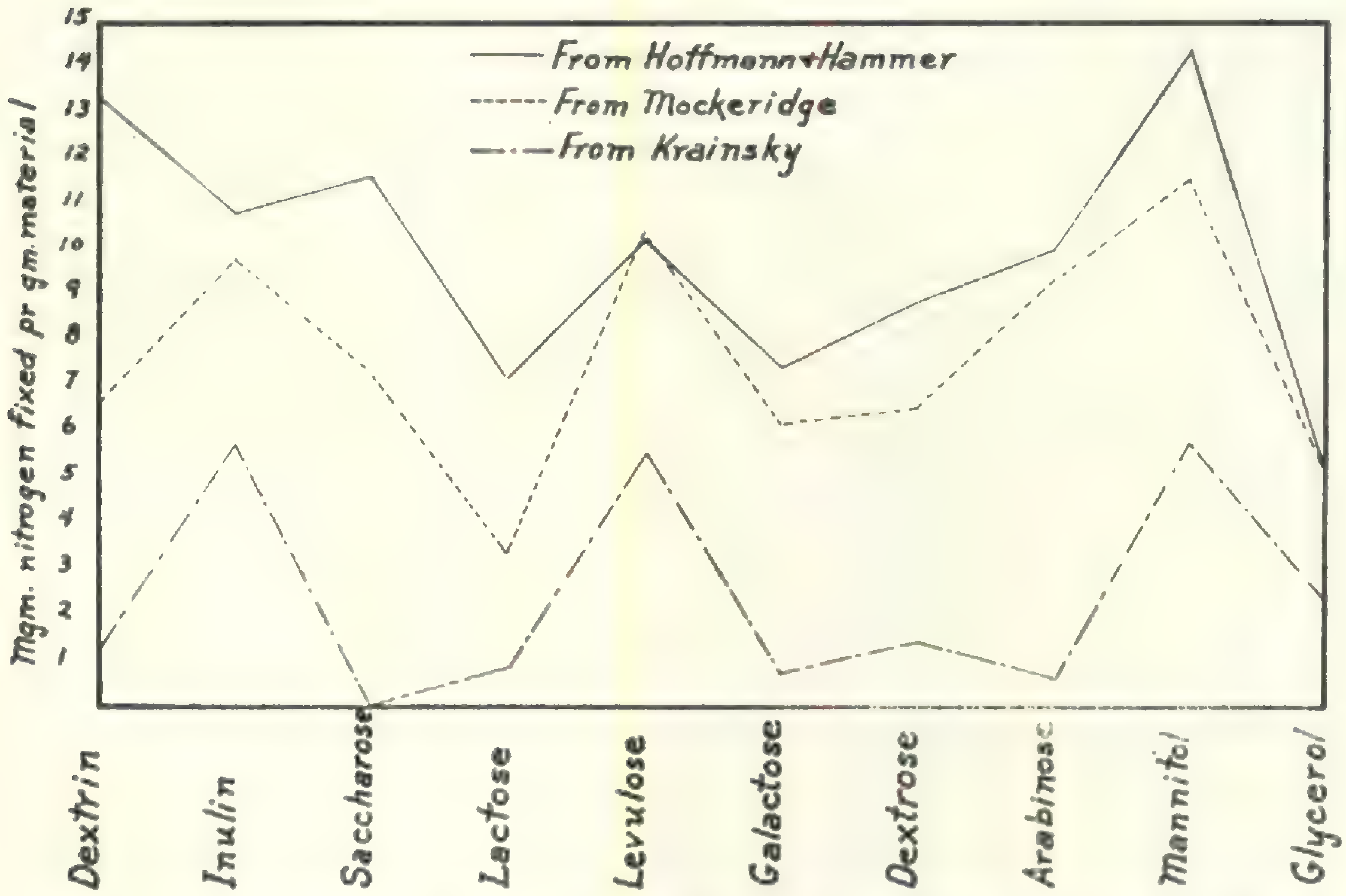

Fig. 3. Showing fixation of nitrogen per gram of organic material, secured by different investigators.

In spite of the numerous possibilities for errors the curves in fig. 3 show a marked qualitative similarity. The absolute quantities of nitrogen fixed per gram of material vary very widely. This might be taken to indicate a variation in the efficiency of the cultures, but, as mentioned in the preceding paragraph, it may merely mean that the organic material was not used up quantitatively in, for example, Krainsky's experiments.

If it is assumed that in all instances approximately the same quantity of organic material was available, and that it was used up quantitatively, then we would be justified in concluding that there are wide variations in the efficiency with which different

cultures utilize the same compounds and also a marked contrast in the efficiency with which the same culture used different organic materials in the fixation of nitrogen. There are strong indications, however, that different cultures may utilize many of the same compounds with approximately the same relative efficiency. Attention was called to this in connection with the experiment reported in table XXIII, in which out of forty cultures tested the quantity of nitrogen fixed, when dextrose served as the organic food, did not vary very widely in most instances.

The work here reported has been confined almost entirely to the salts of fatty acids, principally calcium salts. And attention may be called again to the possible marked effect that the cation may have upon the availability of the fatty acids, as indicated in table IX. It is necessary of course to use the salt of any acid to be tested in order to avoid the inhibiting effect of the hydrogen-ion concentration produced by the free acid. The only previously reported work with which these data can be compared directly is that of Mockeridge, recorded in table XXXII. That portion of Mockeridge's data dealing with fatty acids has been recorded in table XXXIII parallel with a summary of the data presented in this paper. In this table are recorded in parallel columns the molecular weights, heat of combustion, nitrogen fixed per gram of acid consumed, and nitrogen fixed per calory of heat energy contained in the material consumed.

Qualitatively, the only point of difference between the data presented here and those reported by Mockeridge is in the utilization of formic acid. In no instance have either quantitative or qualitative evidence of the growth of any culture of *Azotobacter* in the presence of a salt of formic acid been observed in this work.

Quantitatively, the data agree in showing that as the molecular weight or heat of combustion increases, the quantity of nitrogen fixed per unit of acid consumed increases. This is brought out clearly in fig. 4. There is, however, a difference, possibly significant, in the type of curves plotted from the two sets of data as shown in fig. 4 where the nitrogen fixed is plotted against molecular weight, or heat of combustion, since both increase arithmetically in the compounds as arranged in the figure.

TABLE XXXIII

MOLECULAR WEIGHT, HEAT OF COMBUSTION AND RELATIVE NITROGEN FIXED PER GRAM AND PER CALORY OF ORGANIC ACIDS BY CULTURE NO. 94 (AZOTOBACTER VINELANDII)

Acid	Molecular weight	Heat of combustion	Heat of combustion calories per gram	Mgs. nitrogen fixed per gram	Mgs. nitrogen fixed per calory	Mgs. nitrogen fixed per gm. (Mockeridge)	Mgs. nitrogen fixed per calory (Mockeridge)
Formic	46	61.7	1.34	0.00	0.00	1.47	1.10‡‡
Acetic	60	209.4	3.49	2.60*	0.74	3.77	1.09
Propionic	74	367.4	4.97	5.66†	1.14	5.16	1.04
Butyric	88	524.4	5.96	8.52‡	1.43	6.08	1.02
Valeric	102	681.6	6.68	10.71§	1.58		
Caproic	116	830.2	7.16	17.87§	2.49		
Iso-butyric	88	524.4††	5.96	3.53*	0.60		
Mono-hydrated-valeric	102	681.6††	6.68	5.99§	0.90		
Tri-hydrated-valeric	102	681.6††	6.68	7.49**	1.12		
Iso-caproic	116	830.2††	7.16	7.57*	1.06		
Dextrose	180	677.2	3.76	8.85	2.33	6.57	1.75

* Average of 5 determinations.

† Average of 3 determinations.

‡ Average of 8 determinations.

§ Average of 10 determinations.

** Average of 7 determinations.

†† Assumed to be same as for normal compounds.

‡‡ Recalculated for heats of combustion recorded in table. Mockeridge used different heat of combustion values.

This difference is shown more strikingly in fig. 5 in which the nitrogen fixed is plotted against a unit of energy contained in the compound.

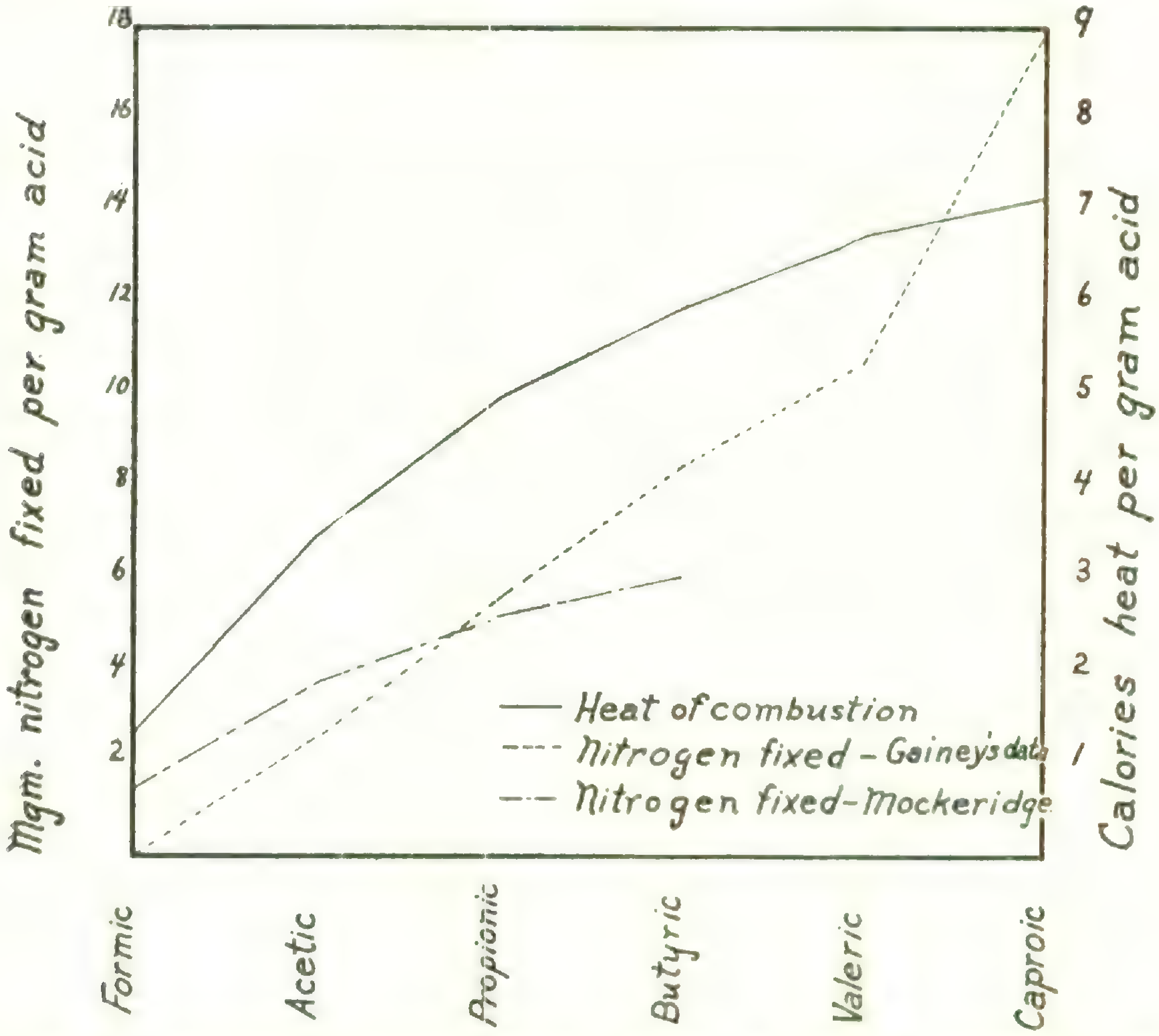

Fig. 4. Comparison between nitrogen fixation and heat of combustion per gram acid.

If the quantity of nitrogen fixed were proportional to the heat of combustion, then in fig. 4 all three curves should run parallel, while in fig. 5, the two lines should coincide and lie horizontal to the base line.

In fig. 4 the nitrogen-fixation curve plotted from Mockeridge's data tends to diverge from the curve for heat of combustion, and in fig. 5 it approaches the abscissa. Such curves would indicate that as the molecular weight increases the quantity of nitrogen fixed per unit of energy decreases. The decrease indicated in Mockeridge's data is very slight and is probably within the limit of error. On the other hand, the nitrogen fixation curve

in fig. 4 based upon new data starts well below the heat of combustion curve and actually crosses it with a marked upward tendency rather than a tendency to flatten out, while in fig. 5, starting on the base line, the curve continually, though not uniformly, rises from formic to caproic acid. Such curves indicate that as the molecular weight increases the organism is capable of utilizing the contained energy more efficiently. Atten-

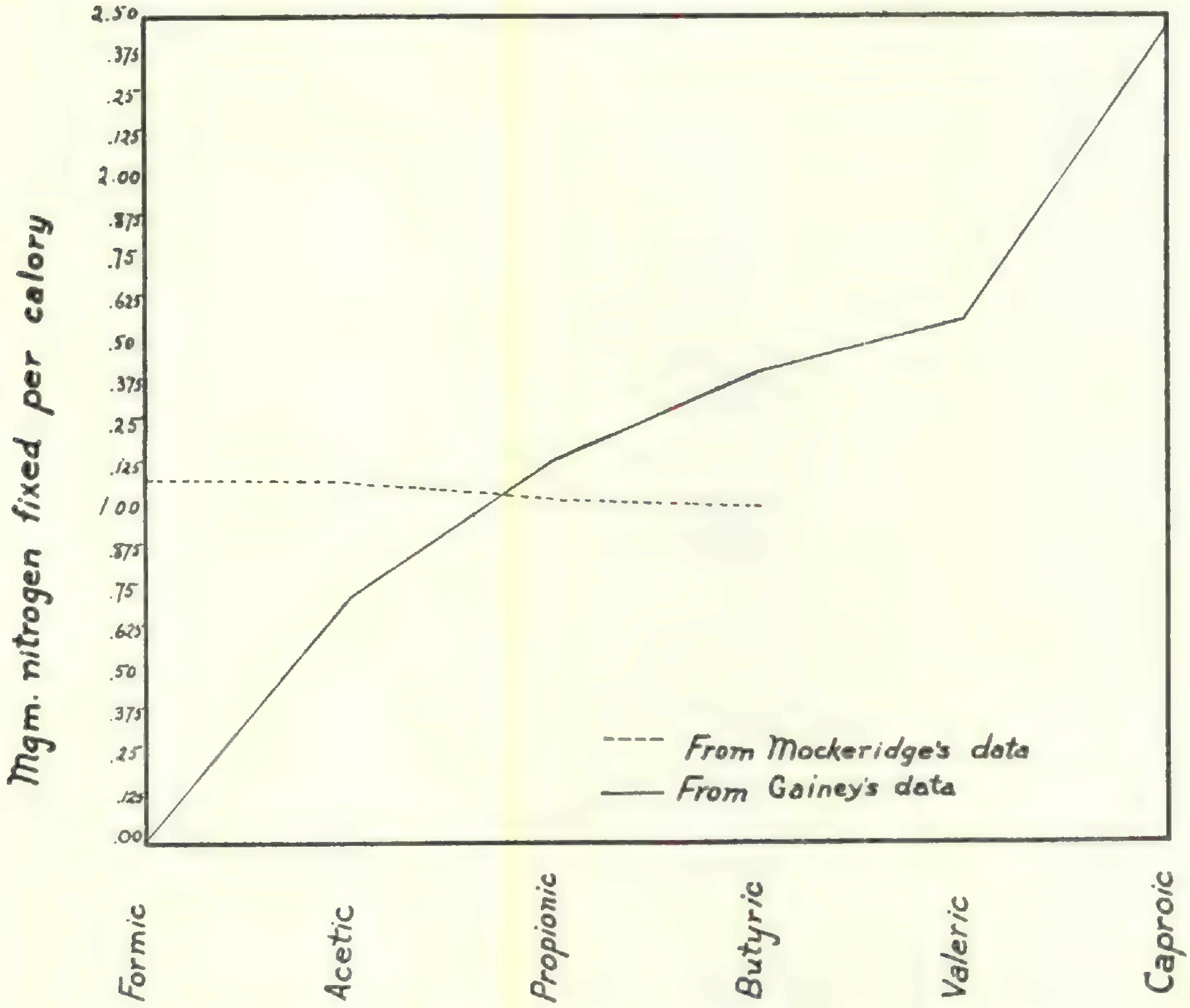

Fig. 5. Showing fixation of nitrogen per calory heat of combustion.

tion has previously been called to the fact that growth has been uniformly more rapid in caproic, and frequently in valeric acid, than in the acids of lower molecular weights.

The data serving as a basis for figs. 4 and 5 were secured from normal acids. In no instance has the iso acid appeared to be used as rapidly as the corresponding straight-chain compound. No explanation is offered as to the reason for this unless it is

that the straight-chain compounds are more frequently encountered by the organisms in nature and as a result they have become better adapted for metabolizing substances of this type. The data presented in table XXXIII indicate the same tendency on the part of *Azotobacter vinelandii* to utilize more efficiently, though not to the same degree, the iso acids of a higher molecular weight.

When the fatty acids are compared with dextrose and their efficiency measured in terms of nitrogen fixed, two points in connection therewith are worthy of note. If the nitrogen fixed per gram of material be used as a basis for comparison dextrose ranks about on a par with butyric acid, acetic and propionic being much inferior, while valeric and caproic, especially the latter, are superior. On the other hand, if the energy content be used as a basis for comparison, then dextrose ranks only slightly below caproic acid.

The data presented in table XXXIII are inconclusive in showing a close correlation between the energy content or heat of combustion of an organic compound and the efficiency with which *Azotobacter* can utilize it as the organic food required; nevertheless, there is more indication of a correlation when compared upon this basis than simply upon the actual weight of the material. There is an urgent need for much more data on the series of compounds herein reported, as well as other series, secured under carefully controlled quantitative conditions with definitely identified cultures, before any very definite conclusions can be drawn as to the energy relations concerned in the fixation of nitrogen by *Azotobacter*.

Summary

The experiments reported in this paper have been carried out with the object of determining the relative ability of different cultures of *Azotobacter* to utilize qualitatively and quantitatively calcium salts of the different fatty acids up to and including six carbon atoms. Two cultures have been studied intensively, others to a less extent. The quantity of acid and total nitrogen present in the medium before and after varying periods of incubation were determined. The rapidity of growth was recorded,

as was also qualitative tests of changes in hydrogen-ion concentration.

The following is a summary of the more important tentative conclusions indicated by the limited experimental data secured:

(a) The various strains of *Azotobacter* behave quite differently with respect to their ability to utilize different fatty acids. Some cultures have been tested that seem rather limited in this respect, while others may utilize all of the acids tested.

(b) Individual cultures may vary widely not only in their ability qualitatively to utilize different acids but there may also be a marked difference quantitatively in this respect.

(c) The iso compounds are not as readily metabolized as are the normal.

(d) There is a marked tendency toward the reduction of the hydrogen-ion concentration in a medium in which an acid is utilized by *Azotobacter*. In some instances, apparently, this phenomenon may be responsible not only for the cessation of growth but actually for the death of the organisms.

(e) The quantity of nitrogen fixed is more or less proportional to the quantity of acid utilized.

(f) The quantity of nitrogen fixed per unit weight of acid consumed increases as the molecular weight or heat of combustion increases, provided comparisons are limited either to normal or iso compounds. There is some indication that the efficiency with which *Azotobacter* can utilize various acids, as measured by the quantity of nitrogen fixed, increases as the molecular weight increases, even when the comparison is based upon the energy content of the material utilized.

(g) The cation with which the acid is combined apparently plays a very important role in determining the ability of an organism to utilize the acid.

(h) The quantity of nitrogen fixed when various acids are utilized is more closely correlated with the energy content than it is with the actual weight of the material consumed.

Acknowledgement

I wish to take this means of expressing my appreciation to the officials of The Missouri Botanical Garden and The Kansas

Agricultural Experiment Station for the valuable aid rendered in making possible this investigation; and especially to Dr. B. M. Duggar under whose guidance the work was undertaken and whose constructive criticism has proved of inestimable value in its prosecution.

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THE EFFECT OF ULTRA-VIOLET RADIATION UPON HIGHER PLANTS[1]

ETHEL TABER ELTINGE

Jessie R. Barr Research Fellow in the Henry Shaw School of Botany of Washington University

Introduction

The sterilizing action of ultra-violet radiation has been known for over fifty years. Downs and Blunt in 1877, working with putrefying material, were the first to discover it. Since then there have been many workers in this field, and to-day ultra-violet sterilization is a more or less common practice.

At present, work with ultra-violet rays is carried on along two different lines. One line deals with the effects produced in higher animals and man with particular reference to the depth of penetration of the rays and to the changes produced within individual cells. The other line deals with the effects produced in plants. Little work was done in the latter subject until 1911 when Kluyver studied the effect on plants of a long-continued raying with an ultra-violet lamp. From then until 1918 the subject received little attention. Since then, however, it has taken on a fresh impetus, and to-day there are many people working in that field. At the present time it is generally known that raying with an unscreened quartz mercury lamp causes injury due to the presence of the short rays. The important line of research now is to determine the effects of the longer ultra-violet rays on the different groups of plants, and this can be done only by the use of specific screens to eliminate certain rays.

Under favorable conditions the spectrum of sunlight contains rays as short as 291 $\mu\mu$. Thus if a mercury vapor lamp is screened to absorb all rays shorter than 291 $\mu\mu$, the same type of rays penetrate as are found in sunlight, the only difference being that

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfilment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany.

the ultra-violet rays are much more intense, since the atmosphere screens out much of this group of rays originally in sunlight.

History

THE EFFECT OF ULTRA-VIOLET RADIATION ON LOWER ORGANISMS

Many articles have been written on the effect of ultra-violet rays on bacteria. Potthoff ('20) found that a suspension of bacteria 3½ mm. thick placed 15½ cm. from the light gave the following results.

LENGTH OF TIME NECESSARY FOR THE DESTRUCTION OF BACTERIA

	Spores	Vegetative cells
B. anthracis	5 minutes	15 seconds
B. subtilis	9 minutes	2 minutes
B. mesentericus	5 minutes	1 minute

In pigmented forms a short exposure inhibited the production of pigment, but upon repeated short exposures the pigment again appeared.

Mashimo ('19) found that the rays most effective in the destruction of bacteria were those between 295 and 186 $\mu\mu$. He proved this by using in a quartz spectrograph a culture of bacteria instead of a photographic plate and noticing the region where no growth appeared.

Bazzoni ('14) found that the destructive power of ultra-violet radiation in relation to bacteria increased rapidly with a decrease in wave length, but that this effect was in some way dependent upon association with longer wave lengths. Wave lengths of from 220 to 225 $\mu\mu$ killed the bacteria after several hours, while the same intensity of light containing full radiation destroyed them very rapidly.

Burge ('17) has proved that ultra-violet rays kill living cells such as bacteria, not by destroying the intra-cellular enzymes but by coagulating the protoplasm. For his work he used bacteria that liquefy gelatin and found that the organisms killed by ultra-violet when ground with sand produced as much liquefaction as ground living organisms.

Green ('97) found that the destruction of diastase in a leaf was less than in an extract of malt or saliva and concluded that

either the chlorophyll or the proteins of the protoplasm must act as a screen absorbing the injurious rays.

Tanner and Ryder ('23) have found that yeast cells are almost as susceptible to ultra-violet radiation as bacteria, although pigmented yeasts are more resistant than white ones.

Nadson and Philippov ('28) used a Bach model of a quartz mercury vapor lamp giving rays as short as 220 $\mu\mu$. Twenty-four-hour cultures of *Saccharomyces* and *Mucor* of different species on nutrient agar were rayed at thirty cm. from the light for ten to twenty minutes. For raying, the cover of the petri dish was removed and replaced by a piece of heavy glass with a circular opening in the center. After several days the region where there was no glass was devoid of growth, but just at the edge of the opening where only the slanting ultra-violet rays and hence the long ones were received, there was a marked increase in growth. Growth under the glass was normal. With yeast, not only increased, but abnormal, budding was noticed in the region of increased growth. With some fungi, asexual reproduction was increased while with others it was the sexual.

Larger organisms have been used for determining the effect of ultra-violet radiation on individual cells. Barr and Bovie ('23) used amoebae that had been cleared through starvation. They found that after an exposure of three-fourths of a second the amoebae ceased to move and after an exposure of one minute they were killed. At first the edge of the organism was irregular, but in a few seconds it became smooth by swelling. If irradiated for three to four minutes the animal swelled and clear spaces appeared between masses of protoplasm. Soon, however, crenulations were present about the border of the organism, giving the appearance of a loss of solution from the inside.

Tshuhotine ('23) thinks the rays first affect the plasma membrane, increasing permeability by coagulating the colloids. Then the surrounding medium enters and precipitates the protein colloids in the cytoplasm which surrounds the colloid particles of lecithin. Soon the base, coline, is formed which increases decomposition, giving OH ions which promote imbibitional swelling of the protein colloids of the cytoplasm until the cell is completely decomposed.

Brooks ('26) found that the shorter the rays, the greater the amount of 2,- 6,-dibromo phenol indophenol penetrating cells of *Valonia*.

THE EFFECT OF ULTRA-VIOLET RAYS UPON HIGHER PLANTS

Bailey ('94) was the first to notice the harmful effect of light on plants. He used an electric arc light and found that if a piece of glass were placed between the light and the plant the injurious effects were modified. He found lettuce and radishes very sensitive to the arc light. A few hours raying caused leaves of *Coleus* to become shiny and lose their purple color when that color was present only in the upper epidermis. When cross-sections of the leaves were examined, the epidermis was found to be collapsed and opaque, coloring the leaf brown. Professor Rowlee, working with Bailey, concluded that the palisade tissue absorbs a large amount of water from the epidermis, due to greater protoplasmic activity, and the epidermis thus emptied collapses.

The next person to do any extensive work on plants was Kluyver ('11), who, using a quartz mercury lamp giving rays of 230 $\mu\mu$ and shorter, gave the plants one long exposure. He verified Bailey's results as to the injury produced in higher plants and its modification by using a screen of thick glass. Only the epidermis of leaves was found to be affected, but in roots and stems the injury was deeper. Anthocyanin was again found to be decomposed by the short rays which do not penetrate. The longer rays were found to have no effect on anthocyanin.

Ursprung and Blum ('17) used a new method for determining injury. After raying plants the desired time the cells were plasmolyzed in sugar solution and then deplasmolyzed if possible in clear water. The less the injury the greater was the per cent deplasmolyzed in water. Epidermis and cuticle were found to exert a little protection. Usually cells containing chlorophyll were more resistant than those lacking it. Diatoms were found very susceptible, due to the large amount of silica in their walls.

Stoklasa ('11) found that a long exposure to ultra-violet radiation injured the epidermal cells but did not harm the chlorophyll in adjacent cells. Etiolated seedlings turned green in two hours

upon exposure to rays of from 400 to 300 μμ, while it took six hours to produce the same result in sunlight.

Schanz ('20) found that when the rays below 320 μμ were cut off the larger part of the red color disappeared from red-leaved lettuce. In like manner he caused the leaves of copper beech to become green.

Sheard and Higgins ('27) reported the effect of ultra-violet radiation on germination and growth of seeds. They used an unscreened quartz mercury lamp and screens of ultra glass, vita glass, and ordinary glass. In general they found that wave lengths of 270–320 μμ delayed the time and lessened the rate of growth, probably because of changes which carried to their extreme eventuate in the coagulation of the seed albumin. Rays of 320–390 μμ were particularly effective in promoting growth. When seedlings of lettuce, radish, and turnip were irradiated one, two, five, and ten minutes, those which normally germinate and grow in darkness showed most rapid germination and best growth when not rayed. Minimum growth was found in seedlings grown in diffused light. Radiation of these seedlings for two to three minutes by a quartz lamp accelerated the germination and subsequent growth as compared with non-rayed seedlings under similar conditions. Thus they state that raying with the near ultra-violet region aids germination and growth of a cell or normal functioning of an organism which is kept under unphysiologic environment.

Russell and Russell ('27), using a Hewittic mercury vapor lamp, found that when etiolated mustard seedlings were given short daily exposures to ultra-violet rays, dwarfing resulted in direct proportion to the length of exposure. Some chlorophyll appeared in all rayed seedlings. In seedlings grown under normal daylight conditions the dwarfing was not as great.

Dane ('27) found that soybeans irradiated by ultra-violet rays were dwarfed and the leaf and stem tissue brittle and stiff. Stems of irradiated plants were 1½ times as great in diameter as those of control plants. Rayed stems were hollow and showed reduction in medullary rays, the meristematic tissue thus remaining active for a much longer time than that in control plants. The ordinary parenchymatous cells of the medullary rays had developed into xylem and phloem.

Beeskow ('27) found that a daily irradiation of more than ½ minute caused injury to soybeans, but that irradiation of ½ minute caused no injury and might stimulate growth. When corn plants were rayed they showed an increased calcium and phosphorus content.

McCrea ('27) grew *Digitalis purpurea* to the ten-leaf stage in a greenhouse glassed with vita glass. She found greater growth and darker color than in control plants. The plants were then put outdoors and when cuttings were taken in August and September, the rayed plants were found to contain an increased amount of digitalin.

Delf and Ritson (Delf, Ritson, and Westbrook, '27) irradiated *Pelargonium*, *Coleus*, *Fuchsia*, *Abutilon*, *Salvia*, and *Trifolium* for various lengths of time and found retarded growth, delayed germination, retarded flower formation, and leaf fall. In addition there was a loss of anthocyanin by *Coleus* and in many cases a deeper green color produced in *Coleus* and other plants. Six-weeks-old seedlings of *Trifolium* when rayed one-half minute daily showed increased growth.

Westbrook (Delf, Ritson, and Westbrook, '27) used different lengths of days in addition to short exposures to ultra-violet radiation. In all cases injury was greater the shorter the day. The injury consisted in the development of thinner leaves with more compact mesophyll and smaller and fewer air-spaces, reduction of mechanical tissue, and collapse of the cells of the upper epidermis followed by a withdrawal of the chloroplastids from the upper ends of the palisade cells.

Tsuji ('18) obtained increased growth and a higher percentage of sugar in sugar cane grown in sunlight and rayed daily with a weak ultra-violet lamp. When pineapples were grown in sunlight plus a daily raying of forty minutes, the pineapples were sweeter, juicier, and larger than normal. When banana leaves and stalks were exposed to ultra-violet rays after being cut they kept fresh longer than similar leaves and stalks not rayed.

Clement ('26) has found that apples rayed for three hours showed a slight yellowing of the green side, and that when these apples were stored the rayed sides did not regain their green color but remained turgid longer than those not rayed.

Nadson and Rochline-Gleichgerwicht ('28), using a Bach model of an ultra-violet lamp emitting rays down to 220 $\mu\mu$, have found that ultra-violet rays cause crystals of calcium oxalate to form in the cells of *Elodea densa*, *Elodea canadensis*, and *Pterygophyllum hepaticaefolium*. These plants were barely covered with water and placed thirty cm. away from the lamp for ten to thirty minutes. The crystals began as small granules, with a chloroplast often as the center, and increased to good size. After two to four days they dissolved simultaneously with the death of the cell. If the cells were treated with a narcotic before raying no crystals were formed.

THE EFFECT OF ULTRA-VIOLET RADIATION UPON ORGANIC MATERIALS

Calabek ('27) determined the effect of ultra-violet rays upon the swelling of biocolloids such as agar. When agar discs were rayed a marked decrease in swelling resulted. It was found that the effect of raying could be preserved in dry agar for several months even if the agar were redissolved. As a result the hypothesis was advanced that the effect of ultra-violet rays upon plants is due to a lowering of the swelling capacity of protoplasm and cell wall in the upper cellular layers of the plant.

Hess ('26) and others have found that when foods are rayed they are rendered rickets-protective. In vegetable foods phytosterol is activated while in animal foods it is the colesterol that is acted upon.

THE PENETRATION OF ULTRA-VIOLET RAYS

Several authors including Henri ('12) have found that the depth of penetration of the shorter ultra-violet rays through the skin is not more than .1 mm. However, for this work dead skin was used.

Macht, Anderson, and Bell ('28), using living anesthetized animals, have found that with an exposure of one minute ultra-violet rays as short as 302 $\mu\mu$ penetrate through living skin that is more than .1 mm. in thickness. When an exposure of two minutes was given rays as short as 280 $\mu\mu$ passed through. They then tested the penetration of rays into the peritoneal cavity of

rabbits and found that with an exposure of two minutes, rays as short as 313 μμ penetrated into the cavity. Next they compared the penetration of living skin with that of dead skin and found the former much more penetrable. When the dead skin was treated with a lipoid solvent it became as transparent to ultra-violet rays as living skin. The pigment in the skin of a negro was found to absorb almost all the short rays. The same result was obtained by injecting a rabbit intravenously with 1 per cent eosin solution.

Statement of the Problem

The problem in this paper is to determine the effect of ultra-violet light as a whole on higher plants, and whether the longer ultra-violet rays stimulate growth in higher plants.

Materials and Methods

experimental

The lamp used for this work was an air-cooled Uviarc quartz lamp from the Burdick Cabinet Co. In the experiments designated as Series I this lamp was used without a screen of any kind. When used in this way the rays given off range from 578 to 200 μμ (5780 A. U.–2000 A. U.) (fig. 1).

When a screen of vita glass from the Hires Turner Glass Co. was interposed between the light and the plants the rays had a range of 578–289 μμ (5780 A.U.–2894 A.U.). The experiments using this screen constituted Series II.

A screen of quartz-lite glass from the American Window Glass Co. interposed between the light and the plant permits the passage of rays ranging from 578 to 313 μμ (5780 A.U.–3136 A.U.). Experiments using this glass are described in Series III.

The ultra-violet rays produced by a quartz mercury lamp may be divided into two groups, first, the abiotic rays (short rays), with wave lengths ranging from 185 to 290 μμ, which are reducing rays and hence killing rays, second, the biological rays (long rays) which range from 290 to 400 μμ. These are oxidizing rays and hence stimulating. The abiotic rays being very readily absorbed by the atmosphere are never present in sunlight when it reaches the earth, and were essentially eliminated where either of the

glass screens was used. The lamp was used at 50 and at 100 inches from the plant both with and without screens.

Although the atmosphere between the lamp and the plant absorbs some of the short rays, the distance of 100 inches is not sufficient to absorb all the short rays, and 50 inches without a screen allows a large percentage of the short rays to reach the plants. When a lamp screened by vita glass is used at a distance of 50 inches from the plants most of the short rays are absorbed, but none of the long ones. The same screen used at 100 inches

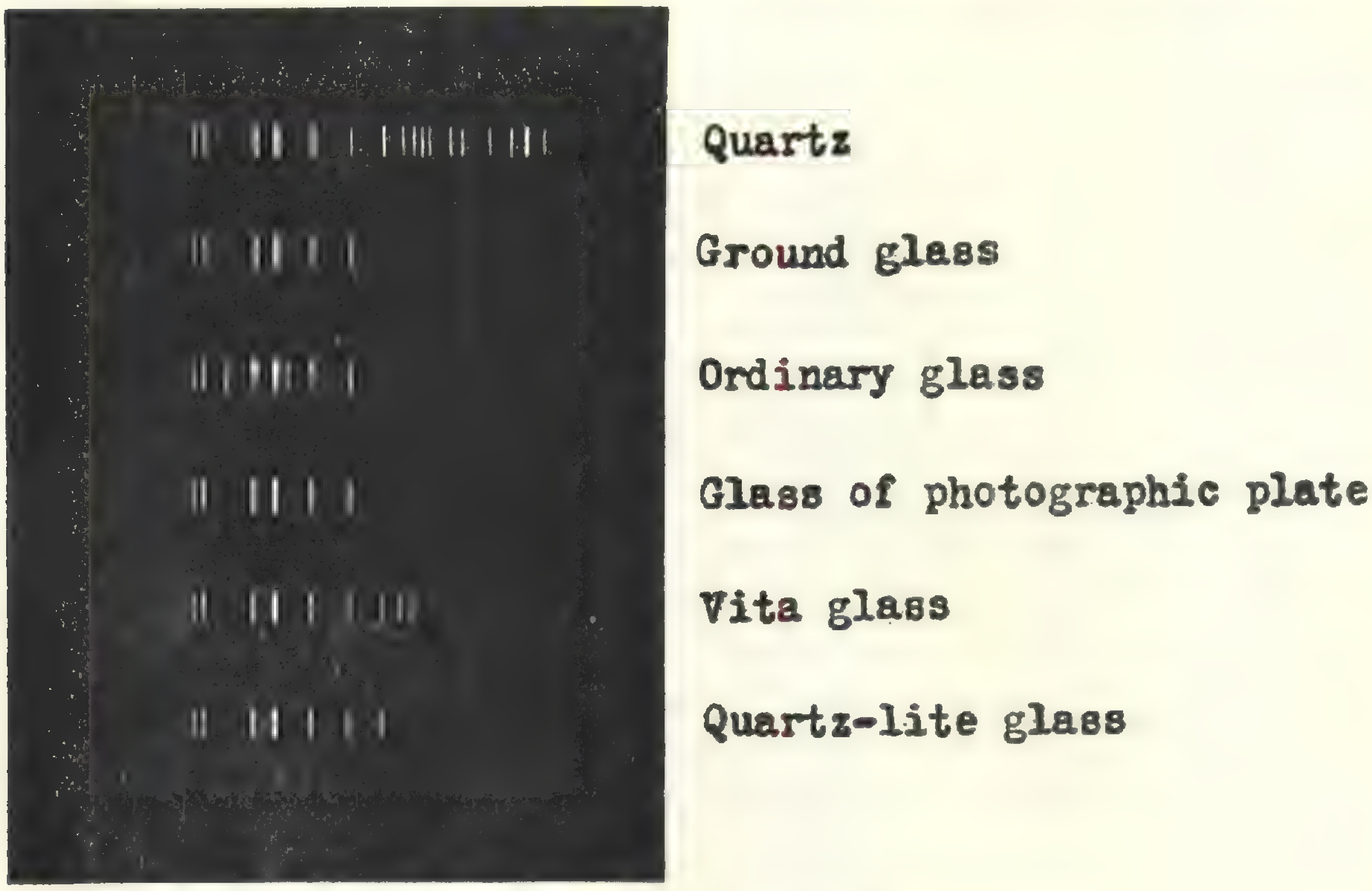

Fig. 1. Showing the spectrum of the different glasses.

from the plants allows only a large percentage of the long rays to reach the plants. When a screen of quartz-lite glass is used instead of vita glass, plants at a distance of 50 inches receive all the long rays and no short ones. The same screen at 100 inches allows only a part of the long rays to reach the plants.

Except for one group of experiments mentioned later the exposure began with 30 seconds the first day and each day was increased that amount. All plants under experiment were moved about each week in the greenhouse to eliminate all differences in environmental conditions.

The plants used were as follows: *Lactuca sativa* L. var. "Black-seeded Forcing"; *Raphanus sativus* L. var. "Early Scarlet Turnip White Tip"; *Cucumis sativus* L. var. "Improved Green Hybrid"; *Ipomoea Batatas* Poir.; *Phaseolus vulgaris* L. var. "Stringless Green Pod"; *Nicotiana Tabacum* L.; *Coleus Blumei* Benth. var. *Verschaffeltii* Lem. and vars. "Spotted Gem," "Defiance" and "Trailing Queen"; *Bryophyllum pinnatum* Kurz.; *Zea Mays* L. var. "Stowell's Evergreen."

Cuttings of *Ipomoea*, *Coleus*, and *Bryophyllum* were made and rooted in sand. They were then planted in rich potting soil in 3- and 4-inch pots. As soon as the plants had recovered from transplanting they were put under the conditions of the experiments. Seeds of *Raphanus*, *Lactuca*, *Cucumis*, and *Nicotiana* were sown in flats. As soon as the plants appeared above ground they were transplanted to 3-inch pots and put under experiment. Seeds of *Zea Mays* and *Phaseolus* were germinated between moist filter-paper and planted in 3-inch pots. All plants when not being rayed were kept under usual greenhouse conditions. A record was kept of the humidity and temperature.

ANATOMICAL METHODS

At the end of four weeks samples of the leaves of the plants rayed without a screen were taken for anatomical study. At the end of eight weeks samples of leaves and stems of all plants were taken for the same purpose. Care was taken in the sampling to take portions which were in corresponding positions on the plants and otherwise as nearly equivalent as possible.

The leaves and smaller stems were killed in medium chromo-acetic killing fluid and imbedded in paraffin. The larger stems were cut free-hand while fresh. Two stains were used: Haidenhain's Iron Haematoxylin and Safranin-Delafield's Haematoxylin.

PHYSIOLOGICAL METHODS

The rate of chlorophyll decomposition under the different screens, in sunlight, and in diffused light was tested, using an 80 per cent alcoholic solution of chlorophyll in vitreosil test-tubes.

The P_H of rayed and control plants in Series I was determined by the colorimetric method. The plant material was pressed in

a mortar and filtered through cotton. Then after diluting 1 to 10 with distilled water the chlorophyll was removed by filtration through an atmometer cup. The indicator was then added to the diluted juice freed from chlorophyll and the result compared with standard tubes.

Starch Storage.—Stem sections were made from fresh material of *Coleus* and *Phaseolus* in the different groups. These were stained with a standard iodine solution to show the distribution of starch.

Dry Weights.—For determination of dry weights plants were dried to constant weight in an oven run at 110° C.

Ash Determination.—Three grams of dry leaf material of the different plants were put into weighed crucibles and burned over a bunsen burner until a large part of the carbon had disappeared. To finish the burning, the crucibles were put into an electric oven at 600° C.

Experimental Observations

SERIES I

For all varieties of plants this series is divided into three parts, group H, which includes the plants rayed at 50 inches from the light; group F, those rayed at 100 inches; and as controls, group G, the same number of plants not rayed.

Series I H (rayed at 50 inches from the light without a screen).—Six young seedlings of *Cucumis* were rayed. The first evidence of the effect of ultra-violet rays appeared on the eighth day, when a slightly shiny appearance of the upper epidermis was noted. By the twelfth day there was evident curling of the edges of the leaf. At the end of three weeks the rolling of the leaves was very evident and the lower ones were turning brown and dying. The young leaves never attained as large a size as those on the control plants. By the end of the twenty-ninth day, when the plants received an exposure of fourteen minutes, one to three flowers were present, but the younger leaves were so rolled that the upper surface was hardly visible. When samples of the leaves were taken at the end of four weeks for anatomical study, they were found to be very brittle. The plant as a whole was very stiff and erect.

The control plants (G) had slightly more leaves and were a little taller. They also had several more flowers. Not only were the leaves greater in number but greater in size, being twice that of the rayed leaves. No rolling of the leaves was noted in the control plants. The color of the leaves was the same in both rayed and control plants except in the older rayed leaves which were brownish.

Six *Ipomoea* plants were used. By the sixth day the younger leaves showed a slightly blistered appearance which increased as time went on. By the eleventh day the veins were brown and the larger leaves showed several brown spots which seemed to be more or less superficial. By the end of three weeks the edges of the leaves had turned down. Very few leaves were shed. At the end of four weeks these leaves were also found to be brittle. The control plants again showed larger and more numerous leaves with no browning.

In the six *Nicotiana* plants, the first effect of raying was noticed on the eleventh day, when the margin of the leaves appeared wavy. By the thirteenth day the edges were definitely rolling upward. About the same time the upper surface became very shiny, and the leaves were so brittle it was almost impossible not to crack them. At the end of three weeks the older leaves were turning yellow and the younger leaves were so rolled that the upper surface was hardly visible, though no leaves were shed. The control plants showed none of these characteristics, the upper surface of the leaves being very hairy and the leaves larger.

The four varieties of *Coleus Blumei* were put into two groups according to their resistance to ultra-violet radiation. The group most sensitive to ultra-violet contained vars. *Verschaffeltii* and "Spotted Gem." At the end of five days a fading of the red color was noticed, and at the end of ten days practically all the red color had disappeared. The glossy upper surface was broken only by the bases of the hairs appearing as dots. The two halves of the leaves were rolled upward toward the midrib and the tips downward, so that the leaves appeared to be only half their normal size and were very brittle (pl. 22, fig. 4). By the end of four weeks all the older leaves had fallen and only a few of the

younger remained and those were very small and abnormal in shape.

The other group containing vars. "Trailing Queen" and "Defiance" seemed to be a little more resistant to ultra-violet rays. Here the first indication of a loss of red color appeared the eighth day. About the same time the shiny dotted appearance of the upper surface of the leaves was observed. The same rolling of the leaves was noted as in the other group. "Trailing Queen" lost very few leaves even at the end of four weeks but var. "Defiance" began to shed its leaves at the end of three weeks.

In the varieties of *Coleus* where any red color was present in the stem a loss of it began to be noted in the tip of the stem at the end of five days and a complete loss at the end of ten days. If after a raying of four weeks these plants were put back under normal greenhouse conditions the red color appeared again to a certain extent in the decolorized tip of the stem and the new growth of stem and leaves was normal.

Ten very young seedlings of *Raphanus* were rayed. At the end of eight days the typical curling upward and shiny appearance of the leaves was noted. Here the rayed leaves seemed to be a little deeper green than the control leaves. At the end of four weeks the leaves and petioles were almost as brittle as the rayed *Nicotiana* leaves. At the end of eight weeks the plants were so curled they appeared almost dead. The roots of the control plants, as well as the leaves, were much larger, as will be seen in pl. 21, fig. 7.

Two sets of *Lactuca*, containing ten plants each, were used, one set having two leaves and the other nine to ten. The object was to see if the older plants would be more resistant to ultra-violet radiation. The set of plants having two leaves never seemed to get much larger, as will be seen in pl. 22, figs. 2 and 3. At the end of two weeks the leaves were noticeably smaller and fewer than on control plants. All the new ones formed were abnormal and the older ones soon dried up and dropped off. As time went on the difference between the rayed and control plants became the most striking of any of the plants tried. At the end of eight weeks the rayed plants had an average of 4.25 leaves per plant while their controls had 13.

This and one set of *Raphanus* plants were the only groups of plants under Series I H that were rayed for eight weeks, the others being discontinued at the end of four weeks. A comparison of these plants at the end of four weeks and eight weeks with similar plants rayed at 100 inches (F) will be seen in pl. 22, figs. 2 and 3.

The set of plants having nine to ten leaves was found to be a little more resistant. At the end of one week the oldest leaves began to show tiny brown spots scattered over their surfaces. Soon after they began to dry up. At the end of three weeks all the older leaves were dead and the new ones smaller but not nearly as small as the new ones in the group having two leaves at the beginning. The leaves were very brittle and even the youngest very curly and brownish (pl. 22, fig. 1). At the end of eight weeks the rayed plants had an average of 18.32 leaves per plant and the controls 25.8 leaves (table I).

TABLE I

SHOWING RATE OF GROWTH IN LACTUCA. FIGURES INDICATE THE AVERAGE NUMBER OF LEAVES PER PLANT

Date	Series number							
	I H		I G		I H		I G	
	Pres.	Lost	Pres.	Lost	Pres.	Lost	Pres.	Lost
Mar. 1	2.00	0	2.00	0	10.00	0	10.00	0
Mar. 8	3.60	0	3.40	0	10.60	2.00	11.60	1.30
Mar. 15	4.60	.60	4.60	0	10.40	4.50	12.20	2.60
Mar. 22	4.00	2.30	6.20	0	10.20	4.40	11.30	4.10
Mar. 29	4.30	3.10	7.00	1.50	12.60	2.10	14.30	1.33
Apr. 5	5.10	.30	8.00	.90	15.10	2.40	18.16	1.00
Apr. 12	5.00	1.10	10.00	1.20	15.66	5.33	21.20	3.90
Apr. 19	4.80	1.20	10.20	2.40	18.33	4.00	25.80	3.90
Apr. 26	4.25	5.00	13.00	1.00				
Net total	2.25	13.60	11.00	7.00	8.33	24.73	15.80	18.13

In *Bryophyllum* the first evidence of raying appeared the sixth day in the form of a glossy upper surface. At the end of two weeks the new leaves were very abnormal in form, the halves rolling upward from the midrib but the leaf itself not curling.

Three sets of *Phaseolus* seedlings were used with six plants in each. One set had both cotyledons intact, another had one

cotyledon removed, and the third had both cotyledons removed. The object was to determine if the removal of stored food had any influence on the effect of raying. In all cases growth was retarded and burning resulted. The leaves became very blistered and abnormal in shape. The difference between rayed and control plants with both cotyledons removed was very great but the difference with one cotyledon removed was about the same as where both cotyledons were intact (table v).

Series I F (rayed at 100 inches from the light without a screen).—The results with *Cucumis* here were in general the same, though never as marked for the same amount of raying, as in Series I H. The appearance of injury was retarded several days, being noted first on the fifteenth day when the plants received an exposure of 7½ minutes. For comparison of the size of rayed and control plants see table II and pl. 21, figs. 1 and 2. At the end of four weeks the average dry weight of rayed plants was 0.616 grams and the control plants 1.29 grams. At the end of eight weeks the leaves were as rolled as in Series I H.

TABLE II

SHOWING RATE OF GROWTH IN CUCUMIS. FIGURES EXPRESS AVERAGES PER PLANT

Date	Series number					
	I F			I G		
	Leaves pres.	Leaves lost	Ht. in cm.	Leaves pres.	Leaves lost	Ht. in cm.
Feb. 1	2.00	0	0	2.00	0	0
Feb. 8	6.00	0	7.35	5.25	0	6.00
Feb. 15	7.00	.75	9.55	7.00	1.25	7.70
Feb. 22	7.50	.20	11.60	8.00	.20	11.25
Feb. 29	9.00	.30	13.80	10.00	.28	14.00
Net total	7.00	1.25	13.80	8.00	1.73	14.00

The experiment using *Ipomoea* plants was continued for eight weeks. A slight browning of the veins was noticed at the end of the eighteenth day when the plants received an exposure of nine minutes. At the end of four weeks the usual blistering appeared as can be seen in pl. 21, fig. 6. About as many leaves were added as to the control plants but they never attained as large a size.

Nicotiana behaved very much the same here as in Series I H except that the effects were a little later in appearing.

The same four varieties of *Coleus Blumei* were used as in the preceding series and were again divided into two groups. The effect on both groups was somewhat less marked and much retarded, particularly as far as shedding leaves was concerned. The more resistant group shed no leaves until the fifth week, and at the end of seven weeks only a few had been shed (pl. 23, figs. 1–4). When these plants were put under normal greenhouse conditions at the end of eight weeks raying, they began to show normal growth and color after ten days, but at the end of four weeks they were still far behind the control plants (pl. 22, fig. 5).

Two sets of *Raphanus* were used, one with two leaves and the other with four to five leaves. Here there seemed to be very little difference in the effect produced whether the plant was just above ground or had several leaves. The effect of raying did not appear until the eighteenth day, but at the end of four weeks it was quite marked (pl. 21, fig. 5). At the end of eight weeks there was a noticeable difference in the number of leaves, the rayed plants averaging 6.2 and the control 8.42 leaves per plant (table III (a), and pl. 21, fig. 4).

The same two sets of *Lactuca* plants were again used. The same general results were found for the set having two leaves, but in the set having nine leaves the rayed plants produced as well as lost more leaves than the controls though they were never as large. A comparison of the effects produced here with those in Series I H can be well seen in pl. 22, figs. 1, 2, and 3 and table III (b). In addition to the above two sets of plants two more sets were used, one set consisting of two-leaved lettuce plants of a red variety and the other of old lettuce plants with fifteen leaves. Red lettuce was rayed to see if the color would disappear as it had done in *Coleus*. However, after raying for eight weeks the red color was still evident though partly masked by the brownish effect of raying. The old *Lactuca* plants were used in order to determine the effect of ultra-violet light on bud and flower formation. The same retarding effect was found though less with these older plants. At the end of eight weeks both rayed and control plants were

budded. The flower stalks of the control plants were greater in diameter and seemed to branch more at the top (pl. 26, fig.1).

Bryophyllum rayed under these conditions showed no curling of the leaves, due no doubt to their thickness. However, the leaves again rolled upward from the midrib. At the end of two weeks they had shiny brownish surfaces similar to those found in many of the other plants, and often parts of the new leaves formed were undeveloped. For a comparison of the rate of growth in rayed and control plants see table III (c) and pl. 26, fig. 5.

The ten *Zea Mays* seedlings were found to be as resistant to ultra-violet light as any of the plants used, showing the first evidence of any harmful effect the twenty-fourth day when they received a twelve-minute exposure. Even then the effect was slight, taking the form of a slight rolling upward of the edges of the leaves. When the rate of growth was compared, the rayed

TABLE III

SHOWING RATE OF GROWTH IN SERIES I F AND G. FIGURES INDICATE THE AVERAGES PER PLANT

Date	(a) Raphanus				(b) Lactuca							
	I F		I G		I F		I G		I F		I G	
	Pres.	Lost	Pres.	Lost	Pres.	Lost	Pres.	Lost	Pres.	Lost	Pres.	Lost
Mar. 1	2.00	0	2.00	0	2.00	0	2.00	0	9.0	0	9.0	0
Mar. 8	4.00	0	3.91	0	3.75	0	3.7	0	12.0	1.50	10.4	2.2
Mar. 15	5.63	0	5.63	0	4.28	0	4.2	0	12.9	2.70	10.6	2.1
Mar. 22	6.90	0.09	6.16	0.03	5.21	1.7	7.0	0	12.9	3.65	10.75	2.3
Mar. 29	6.90	1.00	6.53	0.03	6.07	3.2	7.4	1.7	10.35	5.80	9.6	4.2
Apr. 5	6.60	1.60	6.64	1.06	6.85	1.4	9.2	0.7	12.6	1.80	12.4	1.5
Apr. 12	7.20	1.00	7.71	0.10	8.80	1.7	11.8	0.4	15.5	2.50	15.5	.7
Apr. 19	6.20	1.60	8.42	0.18	8.77	3.3	12.6	2.2	19.0	3.66	18.4	3.5
Apr. 25					11.55	1.6	16.4	1.8	22.1	1.40	20.6	1.5
Net total	4.20	5.29	6.42	1.40	9.55	12.9	14.4	6.8	13.1	23.01	11.6	16.02

Date	(c) Bryophyllum				(d) Zea Mays			
	I F		I G		I F		I G	
	Lvs. pres.	Ht. in cm.	Lvs. pres.	Ht. in cm.	Lvs. pres.	Ht. in cm.	Lvs. pres.	Ht. in cm.
Jan. 24	12.59	13.14	13.71	14.35	....	....	....	....
Feb. 1	13.71	13.85	14.28	15.71	3.25	3.31	3.50	3.62
Feb. 8	14.85	15.14	15.71	17.35	3.75	5.2	4.00	5.37
Feb. 15	15.14	16.21	16.85	18.57	4.50	6.37	5.00	8.00
Feb. 22	17.00	17.04	17.42	19.07	5.00	8.43	6.25	9.94
Feb. 29					6.00	10.60	6.90	14.20
Net total	4.41	3.90	3.71	4.72	6.00	10.60	6.90	14.20

plants showed a noticeable retardation (table III (d) and pl. 26, fig. 4).

SERIES II

Plants in this series were under exactly the same conditions as those in Series I except that here a screen of vita glass was used. The series was again divided into three parts, group A, rayed at 50 inches from the light, group B, rayed at 100 inches, and group E, which was the control for both this series and Series III. All plants rayed were treated daily for seven weeks.

Series II A (*rayed at 50 inches from the light with a screen of vita glass*).—Plants rayed under these conditions responded very differently.

In ten young *Cucumis* seedlings exposed to ultra-violet leaves were produced a little more rapidly than in the control plants (E) but at the end of seven weeks the control plants had slightly more leaves than the rayed ones. The size and color seemed to be about the same for both. The stems elongated almost equally for the first three weeks and then increased very rapidly in the rayed plants, so that at the end of seven weeks they averaged eight to nine centimeters longer and were noticeably greater in diameter than the control plants (table IV (a) and pl. 24, fig. 1). Flowers appeared on the rayed plants two days earlier than on the control plants. At the end of seven weeks the rayed plants averaged 2.3 flowers and the control plants only 1.2 flowers per plant.

Ten cuttings of *Ipomoea* of as near the same size as possible were rayed. Even at the end of seven weeks there was very little difference in height between them and the controls, though the average number of leaves added was much greater in the rayed plants (table IV (b) and pl. 24, fig. 2). The leaves of both rayed and control plants were of about the same size and color.

Observations on fifteen *Nicotiana* plants point toward a retardation of growth, though there was no evidence of any burning. The leaves were about the same in number, size, and color. The stem, however, was taller and smaller in diameter in the control plants. No difference was noticed in the time of

flowering. In general, the rayed plants gave the appearance of being more stocky (table IV (c)).

Ten young *Zea Mays* seedlings were used. At first the control plants grew taller, measuring from the base to the highest node. During the last few days, however, the rayed plants grew very rapidly and surpassed the controls. The rayed stalks were also larger in diameter. The leaves on the rayed plants not only outnumbered those on the control plants, but were from 1.5 to 2.0 cm. wider in the middle, those on the controls averaging 4.0 cm. in width (table IV (d) and pl. 24, fig. 3).

From the very beginning the twenty rayed plants of *Lactuca* produced slightly more leaves than the controls. The leaves of both were the same in color, texture, and size (table IV (e) and pl. 24, fig. 4).

The size of the leaves on the ten rayed *Raphanus* seedlings equalled those on the controls, but there were slightly more leaves on the latter (table IV (f) and pl. 25, fig. 1).

Coleus Blumei vars. "Spotted Gem" and *Verschaffeltii* have been found to be the varieties most sensitive to ultra-violet light, and six cuttings of each as near the same size as possible were used. Both varieties showed the same characteristics. From the very beginning the rayed plants showed greater growth both as to number and size of leaves, and as to height and diameter of stem (table IV (h and i), and pl. 25, figs. 2 and 3). The red color did not seem to be affected as it was in Series I.

Eight cuttings of *Bryophyllum* were rayed. At first the controls grew taller, with a greater number of leaves, but during the last few weeks the rayed plants much surpassed the controls (table IV (g) and pl. 25, fig. 4).

Three sets of *Phaseolus* seedlings of six each were used as in Series I. Those with both cotyledons intact and with one cotyledon removed were taller and had more leaves than the corresponding control plants. Those with both cotyledons removed had slightly more leaves than the corresponding control plants, but were shorter (table V).

Series II B (rayed at 100 inches from the light using a screen of vita glass).—The same number of *Cucumis* plants was used as in Series I A. From the very first the number of leaves on the

rayed plants exceeded those on the controls, but the size of the leaves was about the same in both. The rayed leaves in this group seemed a little deeper green than did the controls. All through the experiment the stems of the rayed plants increased in both length and thickness more rapidly than those of the control plants, and at the end of seven weeks were a little greater in length than the stems of the plants in Series II A (table IV (a) and pl. 24, fig. 1).

About the same number of leaves was present on the ten *Ipomoea* cuttings in this series as in Series II A, which was much greater than in control plants. The stem, however, was greater in length here than in either Series II A or the control E (table IV (b) and pl. 24, fig. 2).

In the fifteen *Nicotiana* plants rayed little difference was found from Series II A either in number or color of leaves or in length and thickness of stem. The control plants had about the same number of leaves but were taller (table IV (c)).

In this group the ten *Zea Mays* seedlings showed a slight increase in number of leaves over those in Series II A and a greater increase over the control plants in E. In average growth in height and diameter of the stalk this group exceeded both the control plants in E and the rayed plants in A (table IV (d) and pl. 24, fig. 3).

Here, as in Series II A, twenty *Lactuca* plants were rayed. All through the experiment there was a slight increase in number of leaves over that in the control plants though the size of the leaves was a little greater in the control plants (table IV (e), and pl. 24, fig. 4).

The ten rayed *Raphanus* seedlings showed leaves equalling those of the control plants in size but fewer in number. The seedlings in this group were almost identical with those in Series II A (table IV (f), and pl. 25, fig. 1).

The same number of *Coleus* cuttings was used as in Series II A. As to number of leaves produced the plants in this group about equalled those in Series II A, but much surpassed the controls in E. Here the plants exceeded in height both those in Series II A and the controls E (table IV (h and i) and pl. 25, figs. 2 and 3).

The *Bryophyllum* cuttings in this group produced about the

same number of leaves as the controls but increased a little more in height than did the controls. Plants in Series II A surpassed this group both in number of leaves and in height (table IV (g) and pl. 25, fig. 4).

SERIES III

The same conditions were present in this series except that instead of vita glass a screen of quartz-lite glass was used. This series also was divided into three parts, group C, rayed at 50 inches from the light, group D, rayed at 100 inches, and group E, again the control. The same number of plants were used in each case as in Series II.

Series III C (plants rayed at 50 inches from the light using a screen of quartz-lite glass).—The number of leaves produced on rayed *Cucumis* seedlings was a little more than in Series II A, but a little less than in Series II B. As to growth in height both Series II A and B surpassed this group by about three centimeters. However, this group surpassed the control by more than five centimeters (table IV (a) and pl. 24, fig. 1).

The *Ipomoea* cuttings in this group produced more leaves than in either A or B of Series II, though the growth in height was a little less here than in those groups. This group showed better growth than the control in all respects (table IV (b) and pl. 24, fig. 2).

There was little difference between the growth of the *Nicotiana* plants here and in groups A and B of Series II. The control plants surpassed all three mentioned groups in height, but about equalled the other groups in number of leaves (table IV (c)).

The *Zea Mays* seedlings here were almost identical with those in Series II B as to number and size of leaves and as to height of plant. It would be hard to determine from external observation which of these two groups produced the better growth (table IV (d) and pl. 24, fig. 3).

The *Lactuca* plants in this group showed more leaves than either the control plants or the plants in Series II A and B. However, the leaves in this group of plants were a little smaller than in the control plants (table IV (e) and pl. 24, fig. 4).

The average number of leaves present in *Raphanus* seedlings in this group was slightly less than in the controls, but otherwise the plants were identical (table IV (f) and pl. 25, fig. 1).

Both varieties of *Coleus* again showed similar results. The cuttings in this group showed more growth in height and number of leaves than did the controls but not as much as in either A or B of Series II (table IV (h and i) and pl. 25, figs. 2 and 3).

The *Bryophyllum* cuttings in this group surpassed the control plants and those in Series II B both in number of leaves and in height. However, the growth in this group did not equal that in Series II A (table IV (g) and pl. 25, fig. 4).

As in Series II A, three sets of *Phaseolus* seedlings were used. Those with both cotyledons intact and with one cotyledon removed were a little taller and had slightly more leaves than the control plants, but were not quite as tall nor did they possess quite as many leaves as those in Series II A. The plants with both cotyledons removed showed less growth in height than the corresponding controls, but a little more than those in Series II A. The number of leaves present differed very little (table V).

Series III D (plants rayed 100 inches from the light using a screen of quartz-lite glass).—*Cucumis* seedlings in this group differed very little from those in group C and thus were several centimeters greater in length than the controls (table IV (a) and pl. 24, fig. 1).

Ipomoea plants showed greater growth in height in this series than in Series III C, with about the same number of leaves present in each series (table IV (b)).

The *Nicotiana* plants closely resembled those in Series II A and B, being stocky while the controls were much taller (table IV (c)).

Seedlings of *Zea Mays* in this group were not quite as tall as in the other groups mentioned, but nevertheless surpassed the control plants. As to number of leaves present this group about equalled the other groups. All the rayed groups in Series II and III, as previously mentioned, possessed leaves from one and a half to two centimeters wider in the middle than the control leaves (table IV (d) and pl. 24, fig. 3).

Lactuca plants in this group gave a slightly smaller count of leaves than in Series III C, but more than in Series II A and B and also more than the control plants. Little difference was noticed between the size of the leaves here and in the control plants (table IV (e), and pl. 24, fig. 4).

Raphanus plants showed slightly fewer leaves than in Series III C and thus fewer than the control plants (table IV (f) and pl. 25, fig. 1).

Both varieties of *Coleus* plants in this group surpassed the control both in number of leaves and growth in height, but showed fewer leaves and less growth in height than in Series II A and B and Series III C (table IV (h and i) and pl. 25, figs. 2 and 3).

Cuttings of *Bryophyllum* showed fewer leaves than in Series II A or Series III C and about the same number as the control plants and Series II B. However, this group showed almost as great growth in height as in Series III C, which surpassed Series II A and B and also the controls (table IV (g)).

TABLE IV

SHOWING THE RATE OF GROWTH OF PLANTS IN SERIES II AND III. FIGURES REPRESENT AVERAGE NUMBER OF LEAVES PER PLANT; AND HEIGHT IN CENTIMETERS

(a) Cucumis

Date	Series II				Series III				Control	
	A		B		C		D		E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 24	2.00		2.00		2.00		2.00		2.00	
Oct. 31	3.50	7.45	3.80	7.60	3.80	6.35	3.60	7.75	3.00	6.8
Nov. 7	5.00	8.90	5.00	10.00	4.90	8.30	5.00	9.85	4.80	7.9
Nov. 14	5.60	9.85	6.00	11.20	5.87	9.50	6.00	10.60	5.77	9.5
Nov. 21	7.10	13.00	6.70	14.00	6.77	11.33	6.80	13.05	5.90	11.1
Nov. 28	7.20	16.90	7.00	19.20	6.77	14.83	6.80	17.15	6.77	13.0
Dec. 5	7.10	22.70	8.11	24.72	7.66	20.00	6.80	22.25	7.44	17.6
Dec. 12	7.30	29.05	8.22	29.77	7.77	26.04	7.10	27.90	7.65	20.5
Net total	5.30	29.05	6.22	29.77	5.77	26.04	5.10	27.90	5.65	20.5

(b) Ipomoea

Date	Series II				Series III				Control	
	A		B		C		D		E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 24	11.12	11.25	7.25	12.82	9.12	8.44	8.25	8.56	5.87	5.75
Oct. 31	14.62	11.50	9.78	13.81	11.87	9.64	10.37	11.37	6.75	6.25
Nov. 7	16.75	12.62	11.75	14.81	13.62	10.59	13.00	12.25	8.50	6.94
Nov. 14	18.25	13.63	14.75	15.21	16.00	11.37	16.25	12.81	10.31	7.97
Nov. 21	20.70	14.50	18.00	16.57	19.87	12.75	17.62	14.06	10.75	8.43
Nov. 28	24.00	15.18	22.00	17.42	24.56	15.21	22.00	15.31	12.75	9.81
Dec. 5	26.75	15.68	25.71	19.57	27.42	16.50	26.06	15.42	14.42	10.35
Dec. 12	28.80	16.50	27.33	20.66	30.14	17.85	31.51	18.00	14.50	10.50
Net total	17.68	5.25	20.08	7.84	21.02	9.41	23.26	9.44	8.63	4.75

(c) Nicotiana

Date	Series II				Series III				Control	
	A		B		C		D		E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 24	4.46		4.10		4.10		4.46		4.46	
Oct. 31	6.40		6.40		6.40		6.60		6.13	
Nov. 7	7.93		7.53		8.06		8.28		7.53	
Nov. 14	9.80		10.07		9.80		9.07		9.21	
Nov. 21	9.50	5.00	9.71	4.89	10.26	5.03	9.70	4.69	9.57	5.85
Nov. 28	10.41	6.12	9.80	6.66	10.58	7.05	9.80	6.65	10.25	8.08
Dec. 5	12.20	9.25	11.90	9.45	12.20	8.95	11.40	9.05	12.55	15.00
Dec. 12	13.20	13.05	13.45	13.45	12.70	13.25	13.20	13.30	12.88	19.05
Net total	8.74	13.05	9.35	13.45	8.60	13.25	8.74	13.30	8.42	19.05

(d) Zea Mays

Date	Series II				Series III				Control	
	A		B		C		D		E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 24	Just above ground									
Oct. 31	3.50	4.62	3.62	5.18	3.38	5.19	3.50	4.62	2.88	4.77
Nov. 7	4.38	7.31	4.88	7.79	4.50	7.87	4.62	7.56	3.80	7.55
Nov. 14	5.12	7.93	5.62	9.43	5.37	9.31	5.25	8.37	5.20	8.60
Nov. 21	5.75	9.43	6.75	12.00	5.66	10.94	6.25	10.68	5.60	10.20
Nov. 28	6.75	12.93	7.85	16.35	7.11	14.61	7.37	14.31	6.40	14.10
Dec. 5	8.00	15.56	8.14	18.57	8.00	17.22	8.33	16.81	7.00	15.80
Dec. 12	9.00	18.75	9.71	20.00	9.22	20.00	9.28	18.42	8.00	17.37

Date	(e) Lactuca					(f) Raphanus				
	Series II		Series III		Control	Series II		Series III		Control
	A	B	C	D	E	A	B	C	D	E
	Lvs.	Lvs.	Lvs.	Lvs.	Lvs.	Lvs.	Lvs.	Lvs.	Lvs.	Lvs.
Oct. 24	8.25	8.10	8.20	8.00	8.10	2.00	2.00	2.00	2.00	2.00
Oct. 31	13.35	12.35	13.15	13.15	12.65	2.80	2.90	2.30	3.30	2.90
Nov. 7	16.90	16.45	16.95	16.45	15.70	4.20	4.40	4.40	4.80	4.20
Nov. 14	20.80	20.45	21.65	20.35	20.25	5.70	6.00	5.40	5.70	5.80
Nov. 21	22.60	23.25	25.20	21.60	20.35	5.80	5.60	5.90	4.70	5.60
Nov. 28	25.61	25.27	25.05	24.52	23.11	5.80	5.60	4.90	5.10	5.37
Dec. 5	27.07	27.78	26.68	29.06	25.85	6.55	6.60	6.10	6.10	7.00
Dec. 12	28.38	27.57	32.18	30.52	26.90	7.22	7.10	6.60	6.40	7.60
Net total	20.13	19.47	23.98	22.52	18.80	5.22	5.10	4.60	4.40	5.60

(g) Bryophyllum

Date	Series II				Series III				Control	
	A		B		C		D		E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 31	9.37	7.46	8.66	5.47	9.33	6.61	8.50	5.34	6.75	5.25
Nov. 7	10.37	7.62	11.00	5.81	10.11	7.05	10.00	5.87	8.00	7.18
Nov. 14	11.37	8.81	11.25	6.75	11.11	8.16	10.75	6.63	9.25	7.75
Nov. 21	12.12	9.87	11.25	7.43	11.90	9.27	11.50	8.00	10.25	7.94
Nov. 28	14.37	10.75	12.12	9.25	13.10	11.44	12.50	10.12	10.75	8.25
Dec. 5	16.28	13.85	13.5	10.68	15.22	11.50	12.75	11.25	11.25	9.25
Dec. 12	18.37	14.94	14.12	12.18	18.00	13.61	14.00	13.37	12.25	10.00
Net total	9.00	7.48	5.46	6.71	8.67	7.00	5.50	8.30	5.50	3.75

(h) Coleus Blumei var. Verschaffeltii

Date	Series II				Series III				Control	
	A		B		C		D		E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 24	7.66	3.75	9.16	4.08	8.83	3.83	9.50	4.00	6.83	3.25
Oct. 31	10.00	4.58	12.00	5.58	10.50	4.83	11.33	5.08	8.33	3.66
Nov. 7	13.66	5.66	17.66	7.83	14.00	6.25	17.16	6.25	11.00	4.66
Nov. 14	18.16	6.46	25.66	9.16	22.50	7.41	26.33	7.75	14.00	5.38
Nov. 21	24.50	8.33	34.00	11.25	32.40	9.40	29.33	9.50	15.50	6.16
Nov. 28	33.66	9.50	43.66	14.91	41.80	10.70	37.66	10.50	19.83	7.58
Dec. 5	40.66	10.66	51.16	16.75	53.60	12.10	43.83	12.66	25.83	10.08
Dec. 12	67.00	14.40	69.30	18.25	64.60	14.30	58.50	14.26	35.16	10.75
Net total	59.34	10.65	60.14	14.17	55.77	10.47	49.00	10.26	28.33	7.00

(i) Coleus Blumei var. "Spotted Gem"

Date	Series II				Series III				Control	
	A		B		C		D		E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 24	10.10	3.33	9.66	3.50	7.00	1.66	6.00	2.00	6.00	2.00
Oct. 31	12.33	6.33	12.00	4.83	7.60	2.08	9.33	2.25	8.66	2.16
Nov. 7	19.60	6.50	20.30	6.50	9.33	2.75	11.00	3.06	10.66	3.00
Nov. 14	24.00	7.58	28.33	7.92	14.00	3.33	16.66	3.33	12.66	3.16
Nov. 21	34.00	9.33	41.00	9.83	20.00	4.50	19.00	4.75	12.66	3.83
Nov. 28	48.30	11.16	51.30	13.33	26.60	5.16	20.00	6.16	15.30	4.83
Dec. 5	58.33	13.16	64.00	16.16	32.00	5.66	22.66	6.83	18.00	6.33
Dec. 12	78.30	15.66	84.00	18.00	36.60	7.16	37.60	8.10	25.66	7.10
Net total	68.20	12.33	74.34	14.50	29.60	5.50	31.60	6.10	19.66	5.10

TABLE V

(a) SHOWING RATE OF GROWTH IN PHASEOLUS SEEDLINGS WITH BOTH COTYLEDONS PRESENT. FIGURES REPRESENT AVERAGE NUMBER OF LEAVES PER PLANT AND HEIGHT IN CENTIMETERS

Date	Series I H		Series II A		Series III C		Control E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 28	2.00	5.25	2.00	4.37	2.00	4.66	2.00	4.21
Nov. 5	3.75	10.37	3.33	10.60	3.50	12.00	3.15	10.75
Nov. 12	5.00	12.75	4.33	13.60	5.00	13.83	4.50	13.37
Nov. 19	5.50	15.00	5.00	17.20	5.10	17.91	4.80	15.71
Nov. 26	5.50	15.80	6.00	22.80	5.30	22.91	5.00	21.08
Net total	3.50	9.55	4.00	18.43	3.30	18.25	3.00	16.87
Av. no. flowers	0		1.6		3.33		1.5	

(b) SHOWING RATE OF GROWTH IN PHASEOLUS SEEDLINGS WITH ONE COTYLEDON REMOVED

Date	Series I H		Series II A		Series III C		Control E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 28	2.00	5.62	2.00	4.16	2.00	4.66	2.00	3.50
Nov. 5	3.25	10.37	3.00	10.40	3.10	9.16	3.30	9.20
Nov. 12	4.00	12.37	4.20	13.00	5.10	12.70	4.00	11.20
Nov. 19	5.00	14.56	4.90	16.40	5.20	13.30	4.50	13.50
Nov. 26	5.00	15.00	5.60	20.70	5.20	20.58	5.00	14.75
Net total	3.00	9.38	3.60	16.54	3.20	15.92	3.00	11.25
Av. no. flowers	0		2.4		.8		1.4	

(c) SHOWING RATE OF GROWTH IN PHASEOLUS SEEDLINGS WITH BOTH COTYLEDONS REMOVED

Date	Series I H		Series II A		Series III C		Control E	
	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.	Lvs.	Ht.
Oct. 28	2.00	5.25	2.00	3.33	2.00	5.33	2.00	4.50
Nov. 5	2.25	8.00	2.50	7.25	2.70	7.46	2.50	8.90
Nov. 12	3.30	9.87	3.60	9.08	4.80	11.00	4.20	12.62
Nov. 19	4.30	11.50	4.20	11.41	4.80	13.40	4.50	14.36
Nov. 26	4.30	11.75	5.10	15.00	4.80	18.50	4.70	18.20
Net total	2.30	6.50	3.10	11.67	2.80	13.17	2.70	13.70
Av. no. flowers	0		.5		.8		1.0	

According to Beeskow ('28) and Delf and Ritson (Delf, Ritson, and Westbrook '27) a daily exposure to ultra-violet of as long as thirty seconds produces no harmful effects in Soy beans and *Trifolium* and might cause a slight increase in growth. Thus several experiments were undertaken to see if this might not be true of other plants. Fifteen young *Nicotiana* plants were rayed at 100

inches from the light without a screen for thirty seconds each day for a period of four weeks. At the end of that time the rayed plants showed a noticeable increase in growth over the control plants (table VI). The same experiment was tried with three varieties of *Coleus* with the same results. Here the increase was not only in number of leaves, but also in height (table VI and pl. 26, fig. 2). Very young lettuce plants were also rayed with the same results.

Next, the exposure of one minute each day at 100 inches from the light was tried on the same three varieties of *Coleus*, with absolutely no change in color. There was, however, a slight retardation in the rate of growth at the end of two weeks, but even at the end of four weeks it was not very noticeable.

TABLE VI

SHOWING RATE OF GROWTH IN PLANTS RAYED 30 SECONDS EACH DAY AT 100 INCHES FROM THE LIGHT, USING NO SCREEN

Date	(a) Nicotiana		(b) Coleus Blumei var. Verschaffeltii			
	Rayed	Control	Rayed		Control	
	Lvs. pres.	Lvs. pres.	Lvs. pres.	Ht. in cm.	Lvs. pres.	Ht. in cm.
Jan. 24	4.26	3.93	12.25	7.50	10.60	7.83
Feb. 1	5.60	5.26	15.50	8.62	11.30	8.00
Feb. 8	7.10	7.13	23.00	10.00	16.60	9.30
Feb. 15	8.46	7.66	28.75	12.12	21.00	10.00
Feb. 22	9.93	8.66	35.45	12.75	29.00	11.30
Total	5.67	4.73	23.20	5.25	18.40	3.34

Date	(c) Coleus Blumei var. "Defiance"				(d) Coleus Blumei var. "Spotted Gem"			
	Rayed		Control		Rayed		Control	
	Lvs. pres.	Ht. in cm.	Lvs. pres.	Ht. in cm.	Lvs. pres.	Ht. in cm.	Lvs. pres.	Ht. in cm.
Jan. 24	11.00	8.37	7.00	4.00	13.50	8.62	15.75	8.87
Feb. 1	14.50	9.50	7.50	4.52	16.25	9.37	18.25	9.25
Feb. 8	19.25	11.87	8.75	6.25	32.75	10.62	33.50	9.75
Feb. 15	24.75	15.00	9.25	8.50	47.00	12.37	44.75	11.25
Feb. 22	26.50	16.50	13.75	10.37	49.75	12.75	50.50	12.00
Total	15.50	8.13	6.75	6.37	36.25	4.13	34.75	3.13

ANATOMICAL

(ALL MEASUREMENTS WERE MADE WITH AN EYEPIECE MICROMETER)

Leaves.—A cross-section of a *Cucumis* leaf rayed under the conditions present in Series I F was measured and found to be a little thinner than a corresponding section from a non-rayed leaf. When the structure of the two sections was compared, it was observed that the rayed section was lacking in upper epidermis, with only the collapsed walls remaining as a false cuticle, which no doubt gave the glossy surface to the leaf. Also the protoplasm in most of the palisade cells had drawn away slightly from the ends of the cells nearest the epidermis. The chloroplastids in the rayed section were found to be more numerous in the ends of the palisade cells nearest the spongy tissue. Another difference was the presence of fewer air-spaces in the rayed section (pl. 28, figs. 4 and 5 and table vii (b)). This corresponds well with the results found by Bailey ('94), Kluyver ('11), and Westbrook (Delf, Ritson, and Westbrook, '27).

When a cross-section of a *Cucumis* leaf, rayed as in Series II A, was measured it was found to be a little thicker than a similar section from a non-rayed plant. A leaf from Series II B was found to be still thicker. It will be remembered that this was also the group where greatest growth in height was found. A leaf from Series III C was thicker than Series II A but thinner than Series II B. A leaf from Series III D was slightly thicker than the control though not as thick as a leaf from Series II A. The control leaf showed very long palisade cells with many air-spaces between them and also among the cells of the spongy tissue. In Series II B where the thickest leaf was found, there were larger air-spaces than in the control leaf. The palisade cells in all rayed leaves in Series II and III were a little shorter than in the control leaves. The thinnest rayed leaf (Series III D) showed fewer air-spaces than the control and instead smaller and more numerous cells. The number and position of the plastids was about the same in all leaves (pl. 29, figs. 1–3, and table vii (k)).

The cross-section of a rayed leaf of *Ipomoea* from Series I H was found to be much thinner than an unrayed leaf. Here, as in *Cucumis*, the epidermis had collapsed, forming a heavy cuticle.

Occasionally, however, an epidermal cell remained intact. The protoplasm of a few of the palisade cells had drawn away from the end nearer the epidermis, and the cells themselves were shorter. A section from an *Ipomoea* leaf in Series I F proved to be of the same thickness as the one from Series I H. Here, however, the epidermis was not collapsed but thinner, each cell being absolutely distinct. The palisade cells were longer than in Series I H but not as long as the controls. There were fewer air-spaces here than in either the control leaf or the leaf in Series I H. This is probably due to the fact that Series I F was rayed for a period of eight weeks and Series I H for only four weeks (table VII (d)).

When rayed *Ipomoea* leaves from Series II A were examined, they were found to be thinner than control leaves. Leaves from Series II B were slightly thinner than those in II A. The palisade cells in both the above-mentioned groups were thinner than palisade cells in control leaves, as were also the upper epidermal cells.

Rayed leaves in Series III C about equalled the control leaves in thickness and length of palisade cells, though the upper epidermis here was still thinner than in the control leaves. Leaves from Series III D were by far the thickest in any of the series. Here the palisade cells and epidermal cells were also longer than in any of the other groups. Air-spaces were found to be much greater and more numerous than in sections of control leaves. Chloroplastids seemed to be more numerous here also (table VII (p), and pl. 29, figs. 4 and 5).

The cross-section of a rayed *Nicotiana* leaf from Series I H was again found thinner than an unrayed leaf. The same collapsing of the epidermis and shrinking of the protoplasm in the palisade cells were also found (pl. 27, fig. 7, and table VII (e)).

Rayed *Nicotiana* leaves from Series II A and B and III C were about the same thickness as those of non-rayed plants. The palisade cells from Series II A and B were a little longer than corresponding cells in a control leaf. A *Nicotiana* leaf from Series III D proved to be much thicker than one from any of the other groups mentioned. Also its palisade cells were longer, and it contained many more air-spaces. However, the upper epidermis

was thinner here than in a non-rayed leaf (pl. 27, figs. 5 and 6, and table VII (o)). It will be remembered that this group, while it did not show greatest growth in height, was the most stocky in appearance and produced flowers at the same time as did the control plants showing greatest growth in height.

When cross-sections of *Zea Mays* leaves were examined it was found that all rayed leaves in Series II and III were much thicker than non-rayed ones, the thickest being present in Series III C, which was rayed for seven weeks at 50 inches from the light using a screen of quartz-lite glass. These leaves also showed the thinnest epidermis and the best-developed vascular bundles. Leaves in Series II A and B were next in thickness, and both had well-developed bundles. Leaves in Series III D were the nearest like those of the control plants, having very thick epidermis and less well-developed bundles. In general, there seemed to be a thicker cuticle present in rayed leaves than in control leaves (pl. 32, figs. 1–6, and table VII (n)).

Cross-sections of *Coleus* leaves in Series I H which were rayed at 50 inches without a screen showed the same collapsed epidermis and lack of air-spaces as were found in similarly treated leaves of other plants. However, here in addition there was a loss of red color. Not only did the color disappear from the epidermis when it collapsed, but also from the palisade cells, showing that the rays penetrate beyond the epidermis or else produce some substance which does. This corresponds well with the results found in animal tissue by Macht, Anderson and Bell ('28) (pl. 31, figs. 4 and 5).

Non-rayed *Coleus* leaves were found to be much thicker than those rayed. The thinnest leaves were found in Series II B, where there was also the greatest growth in height. According to increasing thickness the groups may be arranged as follows; Series II B, II A, III C, III D, and last, the control E. The palisade cells were shorter in Series II B than in any of the other groups, even including the control plants. There was absolutely no decrease in red color in any of the rayed plants in Series II and III. It appeared that in *Coleus* plants the growth in height was inversely proportional to both the thickness of the leaves and the number of air-spaces present (pl. 30, figs. 1–5, and table VII (l)).

Lactuca leaves rayed as in Series I H showed the characteristic collapse of at least part of the epidermis and the lack of air-spaces. In addition, there was no differentiation of palisade tissue. Leaves rayed as in Series I F for four weeks were similar to the controls except that they were a little thinner and developed palisade and epidermal cells that were a little shorter. The air-spaces were also fewer here than in control leaves. If their leaves were rayed for eight weeks instead of four, they were still thinner, had no well-defined palisade layer, and almost no air-spaces. In thickness they about equalled the leaves in Series I H.

When rayed *Lactuca* leaves from Series II and III were examined they were all found to be of about the same thickness and much thinner than corresponding control leaves. The palisade and epidermal cells were also shorter than those present in the control leaves.

Cross-sections of rayed *Raphanus* leaves in Series I F were only very slightly thinner than those of corresponding control leaves. There was the same collapse of epidermis, forming a false cuticle as in other leaves mentioned. The contents of the upper layer of palisade cells had disappeared, leaving them empty. Leaves in Series I H showed about the same injury as those in Series I F rayed for eight weeks. Rayed leaves in Series II and III were all thinner than similar control leaves, those in Series III D being the thinnest. The palisade and epidermal cells, however, seemed to be longer than in the control leaves. This would indicate fewer air-spaces in the rayed leaves in Series II and III than in corresponding non-rayed leaves.

Sections of *Bryophyllum* leaves rayed under the conditions of Series I H were also thinner than corresponding sections of non-rayed leaves. The characteristic lack of upper epidermis was observed and also a thicker under epidermis. Sections of leaves from this plant in Series II A were much thinner than those of control leaves, and there was no collapse of upper epidermis. Leaves from Series II B were about the same thickness as control leaves, but the epidermis was slightly thinner. Leaves in Series III C were thinner than in Series II B but thicker than in Series II A. Leaves from Series III D had longer upper epidermal

cells and were much thicker than any of the other leaves including the controls.

Cross-sections of *Phaseolus* leaves in Series I F were thinner than sections from control leaves. The epidermis was destroyed in some places, but in others the epidermal cells still remained intact. The contents of the palisade cells were much shrunken and the cells shorter. The chloroplastids were also collected in the end of the cells nearest the spongy tissue. Sections of *Phaseolus* leaves from Series II A were much thicker than control sections. They also had longer palisade and epidermal cells and more numerous air-spaces and chloroplastids. *Phaseolus* leaves from Series III C were also thicker than non-rayed leaves but not as thick as those in Series II A (pl. 28, figs. 1–3, 6, and table vii (c and m)).

TABLE VII

SHOWING THICKNESS OF LEAVES AND LENGTH OF CELLS IN MILLIMETERS FOR RAYED AND CONTROL PLANTS. CELL LENGTH TAKEN NORMAL TO LEAF SURFACE

	(a) Lactuca				(b) Cucumis		(c) Phaseolus		(d) Ipomoea		
	Con.	Series I			Con.	Series I	Con.	Series I	Con.	Series I	
	G	F	F'*	H	G	F	G	F	G	F'	H
Leaf	.1279	.101	.076	.074	.1247	.1226	.0938	.0814	.1565	.117	.117
Palisade	.0298	.021	.0156	.014	.045	.045	.0384	.0296	.0408	.034	.029
Upper epid.	.0138	.0137	.0109	.0107 or (—)†	.0135	(—)	.0119	(—) or .0114	.0243	.012	(—)
Lower epid.	.0107	.0091	.0107	.009	.0068	.0126	.0098	.0102	.0239	.011	.0145

	(e) Nicotiana		(f) Bryophyllum		(g) Raphanus		(h) Raphanus				
	Con.	Series I	Con.	Series I	Con.	Series I	Series II		Series III		Con.
	G	H	G	H	G	F'	A	B	C	D	E
Leaf	.143	.1326	.460	.4338	.1604	.1612	.1582	.158	.149	.1293	.163
Palisade	.0525	.0529	(—)	(—)	.0495	.0635	.0495	.049	.047	.0411	.038
Upper epid.	.0218	(—)	.0153	(—)	.0142	(—)	.0148	.019	.015	.0134	.013
Lower epid.	.011	.0112	.0121	.0145	.0151	.0123	.01176	.0103	.009	.0117	.007

	(i) Lactuca					(j) Bryophyllum				
	Series II		Series III		Control	Series II		Series III		Control
	A	B	C	D	E	A	B	C	D	E
Leaf	.0884	.087	.0896	.0882	.1013	.360	.522	.4464	.8075	.5103
Palisade	.0182	.0207	.0204	.0176	.0263					
Upper epid.	.0128	.0154	.012	.0134	.0154	.0153	.0189	.0202	.0153	.0207
Lower epid.	.0078	.0109	.0092	.0089	.0126	.0121	.0099	.0126	.0144	.0121

* F′, plants rayed 8 weeks at 100 iches without a screen.
† (—), lacking.

	(k) Cucumis					(l) Coleus				
	Series II		Series III		Control	Series II		Series III		Control
	A	B	C	D	E	A	B	C	D	E
Leaf	.1307	.1397	.1363	.127	.1257	.1181	.1056	.1232	.1374	.138
Palisade	.0448	.0459	.0454	.0453	.0484	.0364	.0299	.037	.0371	.0375
Upper epid.	.0134	.0096	.0117	.0133	.0126	.021	.0184	.0159	.0156	.0168
Lower epid.	.007	.0117	.007	.0071	.0072	.0086	.0078	.0103	.007	.0112

	(m) Phaseolus					(n) Zea Mays				
	Series II		Series III		Control	Series II		Series III		Control
	A	B	C	D	E	A	B	C	D	E
Leaf	.1369		.1016		.0915	.1408	.1402	.1467	.1366	.1195
Palisade	.0518		.038		.036					
Upper epid.	.018		.0111		.010	.0263	.0260	.020	.0296	.0274
Lower epid.	.012		.0069		.0067	.0204	.0304	.026	.0196	.019

	(o) Nicotiana					(p) Ipomoea				
	Series II		Series III		Control	Series II		Series III		Control
	A	B	C	D	E	A	B	C	D	E
Leaf	.143	.143	.1444	.1584	.145	.1206	.1184	.1316	.168	.133
Palisade	.0525	.0498	.0362	.0487	.0414	.0355	.0375	.0467	.0604	.0476
Upper epid.	.0218	.019	.0148	.0162	.0207	.0179	.0193	.0188	.0243	.0226
Lower epid.	.011	.0112	.0142	.0086	.0103	.0168	.017	.0176	.0212	.017

Stems.—Cross-sections from the base of non-rayed *Cucumis* stems seven weeks old were found to have smaller diameters than any of those from rayed stems. Similar sections from the base of *Cucumis* stems in Series II A and III D were found to be a little broader, while those in Series II B and III C had the

greatest diameter (table VIII). Series II B had the thickest leaves and the greatest growth in height. All rayed *Cucumis* stems in Series II and III also showed larger bundles than control stems, though there was little difference between the different rayed groups. The average width of the rayed bundles from the outside of the stem toward the center was 0.54 mm. and that of similar control bundles was 0.36 mm. The amount of bast tissue was about the same for control as for rayed stems.

Cross-sections from the base of stems of control *Nicotiana* plants were also found to be smaller in diameter than most of the rayed ones. Series II A developed stems a little smaller in diameter than those of the control plants. Stems in Series II B and III C were larger in diameter, and those in Series III D were still larger. It will be remembered that this was the group of tobacco plants that showed the thickest leaves and the healthiest appearance (table VIII). As to development of vascular tissue the control plants again had the thinnest vascular cylinders which were 0.36 mm. in thickness. Next in order of thickness came Series II A (0.378 mm.) followed by Series III C (0.505 mm.) and III D (0.54 mm.). The tracheae were also smallest in the control plants and largest in Series III D with Series II A, B, and III C intermediate and equal. In all cases the walls of the tracheae were thicker in rayed plants than in non-rayed ones.

When sections from the bases of rayed *Zea Mays* stems of the different series were measured, it was found that those in Series II A were a little smaller in diameter than those from the control stems. Series II B had stems a little larger and III D still larger than those in Series II B. Stems in Series III C were the largest of all. This was also the group of plants that showed the thickest leaves and the greatest growth.

There was a noticeable range of variation present in the vascular bundles of the different groups of *Zea Mays* plants. Rayed stems in Series II A showed bundles smaller than those of the control stems, both as to entire bundle and as to size of vessels, but the phloem was better developed than in control stems. Series II B showed bundles of about the same size as control stems, but here the phloem was as well developed as in Series II A and the mechanical tissue much better developed than in

either the control stems or those in Series II A. The best-developed bundles were found in Series III C. Here the phloem and mechanical tissue were very well developed. The walls of the vessels were much heavier here than in any other group of *Zea Mays* plants. The pith cells in the control plants and those in Series II A were angled, while those in Series II B and III C and D were oval in shape, showing more air-spaces. The oval pith cells were also larger than corresponding angled ones. Series III C was also found to have many more layers of cells making up the cortex than any of the other groups of *Zea Mays* plants (pl. 33, figs. 1–8, and table VIII).

When sections of *Coleus* stem from the different groups of plants were measured, it was found that the control plants again showed smaller stems than any of the rayed plants. The stems largest in diameter were found in Series II A and B. It was these two groups also that showed the greatest growth in height (table VIII). The radial diameter of the vascular bundles of the control stems was 0.495 mm., while that of Series III D was 0.612 mm., that of III C, 0.62 mm., and of Series II B, 0.675 mm. This corresponds well with the fact that greatest growth in height was found in this group. Bast tissue was present about equally in all rayed and control stems of *Coleus.*

Sections of *Phaseolus* also showed the control plants to have stems smaller in diameter than any of the rayed plants. Series II A has stems having the greatest diameter. It will be remembered that this group of *Phaseolus* plants also showed the thickest leaves. Series III C had stems just a little smaller in diameter than those in Series II A (table VIII). When the

TABLE VIII

SHOWING THICKNESS IN MILLIMETERS OF RAYED AND NON-RAYED STEMS

Plant	Series II		Series III		Control
	A	B	C	D	E
Cucumis	5.0	5.5	5.5	5.0	4.0
Nicotiana	8.8	9.5	9.5	10.0	8.5
Zea Mays	8.0	8.8	10.7	9.5	8.5
Coleus	6.0	6.0	5.5	5.5	4.8
Phaseolus	3.8		3.5		3.0

vascular cylinder in the different rayed groups was compared it was found to be by far the thickest in Series II A and III C, averaging 0.54 mm. in diameter, while that of the control stems averaged 0.49 mm.

PHYSIOLOGICAL

Chlorophyll decomposition.—A medium green 80 per cent alcoholic chlorophyll solution was made from *Nicotiana* leaves and put in test-tubes of pure fused silica. These were placed horizontally in white dishes and exposed to the different conditions, with results given in table IX.

TABLE IX

SHOWING THE AMOUNT OF TIME NEEDED TO DECOLORIZE CHLOROPHYLL SOLUTION

	9 a.m.	12 m.
Sunlight in greenhouse	12 min.	6 min.
Sunlight outside	4 min.	2 min.
Diffused light in greenhouse	35 min.	18 min.
At 30 inches from an unscreened lamp in diffused light	39 min.	20 min.
Ultra-violet lamp screened with vita glass plus diffused light	40 min.	22 min.
Sunlight outside under a screen of vita glass	6 min.	3 min.
Sunlight outside under a screen of quartz-lite glass	5 min.	2½ min.

These results show plainly that ultra-violet rays do not hasten the decomposition of chlorophyll. Vita glass is thicker than quartz-lite, and hence used at close range the difference in thickness would account for the longer time required for the decomposition under vita glass in sunlight.

Starch storage.—Sections of *Coleus* stem at the end of seven weeks showed more starch in control plants than in any of the plants rayed as in Series II and III. It was impossible, however, to distinguish between the different rayed stems.

In sections of *Phaseolus* stem starch was present in the cortex of plants rayed as in Series II A, while similar control plants showed very little if any starch in the cortex.

Determination of P_H.—*Lactuca* plants under experiment for eight weeks as in Series I F were used for this work, the leaves and stems being determined separately. The P_H of the leaves and stems of both rayed and control plants was found to be 6.0.

The P_H of leaves and roots of *Raphanus* was determined sepa-

rately, and here again the rayed and control plants responded alike, that of the leaves being 6.2 and the roots 6.0. Thus raying with ultra-violet rays seems to have no effect on the P_H of plants.

Dry weights.—In the experiments carried on in 1926 to 1927 as described in Series I, which consisted of plants rayed with an unscreened lamp, dry weight determinations were made of the entire tops of *Lactuca* and both tops and roots of *Raphanus*. In all cases greater dry weight was found in the control plants. This can be well seen in the results in table x (a) and (b).

TABLE X

SHOWING IN GRAMS THE DRY WEIGHT OF PLANTS IN SERIES I H (50 INCHES), F (100 INCHES), AND G (CONTROL)

(a) Raphanus

	4 weeks		4 weeks		8 weeks	
	H	G	F	G	F	G
Tops	.36	.69	.326	.49	.586	1.0
Roots	.41	.79	.126	.174	.24	.496

(b) Tops of Lactuca plants

	2 leaves		9 leaves		2 leaves		9 leaves	
	H	G	H	G	F	G	F	G
4 weeks	.018	.244	.805	2.22	.116	.24	.81	1.24
8 weeks	.003	.770	.825	3.85	.200	1.15	1.56	2.76

In the experiments carried on in 1927 to 1928 the dry weight was determined for fifty grams of wet weight of leaves.

Rayed *Zea Mays* plants of Series II and III showed greater dry weight than corresponding control plants. Series II A showed the smallest dry weight of the rayed plants which was where the poorest growth in rayed plants of Series II and III was found.

Lactuca plants in Series III D had the greatest dry weight. Those in Series II A and III C showed smaller dry weight than the control plants.

Ipomoea plants in Series III D had the greatest dry weight. It was also in this group that greatest growth and thickest leaves were found.

Nicotiana plants showed greatest dry weight in the control plants and the smallest in Series II A.

Cucumis plants had the smallest dry weight in Series II B, and in this group were the greatest growth and thickest leaves with the largest air-spaces.

Phaseolus plants in Series II A showed the greatest dry weight and also the thickest leaves.

Plants of *Raphanus* showed the greatest weight in Series III C and D and the next greatest in the control plants.

Bryophyllum plants also had the greatest dry weight in Series III C and D, though all rayed plants in Series II and III had greater weights than similar control plants. A comparison of the dry weights of the various plants will be found in table XI.

TABLE XI

SHOWING THE DRY WEIGHT IN GRAMS PER FIFTY GRAMS OF WET WEIGHT OF PLANTS IN SERIES I (RAYED WITHOUT A SCREEN), SERIES II (SCREEN OF VITA GLASS) AND SERIES III (SCREEN OF QUARTZ-LITE GLASS)

Plant	Series I	Series II		Series III		Control
	H	A	B	C	D	E
Zea Mays	6.0331	5.462	6.1496	5.8290	5.9232	5.2030
Lactuca	3.1950	2.2307	2.8396	2.3322	3.2320	2.7959
Ipomoea		7.4775	7.0642	7.6735	7.7290	7.3554
Nicotiana		5.3150	5.5130	5.9240	5.9675	6.3225
Cucumis		4.8072	4.5494	4.7149	4.7544	4.8420
Phaseolus		6.9050		5.3994		6.3695
Raphanus		3.8845	3.9775	4.3200	4.3410	4.1361
Bryophyllum	2.8295	3.5100	3.4055	4.2975	3.7585	3.5286

Ash determination.—The results were not conclusive, but they point toward an increase in ash in plants rayed with an unscreened lamp. In plants rayed with a screened lamp the ash was, in the majority of cases, less than in the control plants. In *Cucumis* plants showing best growth there was less ash and also smaller dry weight than in the control plants. This can be explained, however, by the presence of many large air-spaces in those leaves while in the control leaves the air-spaces were smaller.

In *Phaseolus* the amount of ash again corresponded very well with the dry weights, there being the greatest dry weight where there was the greatest amount of ash. This also corresponded with the thickness of the leaves. For comparison of the results see table XII.

TABLE XII

SHOWING THE WEIGHT IN GRAMS OF ASH FOR 3 GRAMS OF DRY LEAF MATERIAL

Plant	A	B	C	D	E	F
Zea Mays	.310	.272	.269	.295	.325	.349
Lactuca	.600	.610	.611	.581	.595	.565
Ipomoea	.410	.302	.395	.392	.505	
Nicotiana	.527	.533	.505	.515	.570	
Cucumis	.562	.521	.505	.530	.599	
Phaseolus	.464		.435		.455	
Raphanus	.638	.630	.643	.558	.789	
Bryophyllum	.564	.5193	.482	.430	.540	.610

The effect of ultra-violet radiation upon transpiration.—When leaves of *Phaseolus, Cucumis, Lactuca* and *Coleus* were placed in bottles of water, sealed with paraffin, and rayed at 50 inches from the unscreened lamp, it was found through weighings taken every 30 minutes of bottles and leaves combined that at first the rayed leaves lost as much as the controls. Then there was a time when less weight and sometimes no weight was lost by rayed leaves. After that there was a loss equalling that of the control leaves kept in darkness or in some cases surpassing it. When the stomata were examined at the end of three hours those in the rayed leaves were found to be closed, while those in the leaves kept in darkness were partly open. When the rayed and control leaves were weighed at the beginning and end of the experiment, it was found that all the rayed leaves had lost weight while the controls had remained constant (fig. 2). It will be noted that *Coleus* behaved a little differently than did the other leaves used. This might be explained by the fact that *Coleus* has stomata on the under surface only. This experiment was repeated several times with the different leaves.

The petioles of leaves of *Coleus Blumei* var. *Verschaffeltii* were paraffined and the leaves placed in a horizontal position, some being rayed on the upper side, some on both sides, and others placed in darkness, Those in darkness and those rayed on the upper surface were partly wilted at the end of twelve hours while those rayed on both sides were still turgid. When weighed, however, the leaves rayed on both sides and those upon one side only were found to have lost much more weight than the leaves kept in darkness (table xiii, and pl. 26, fig. 3).

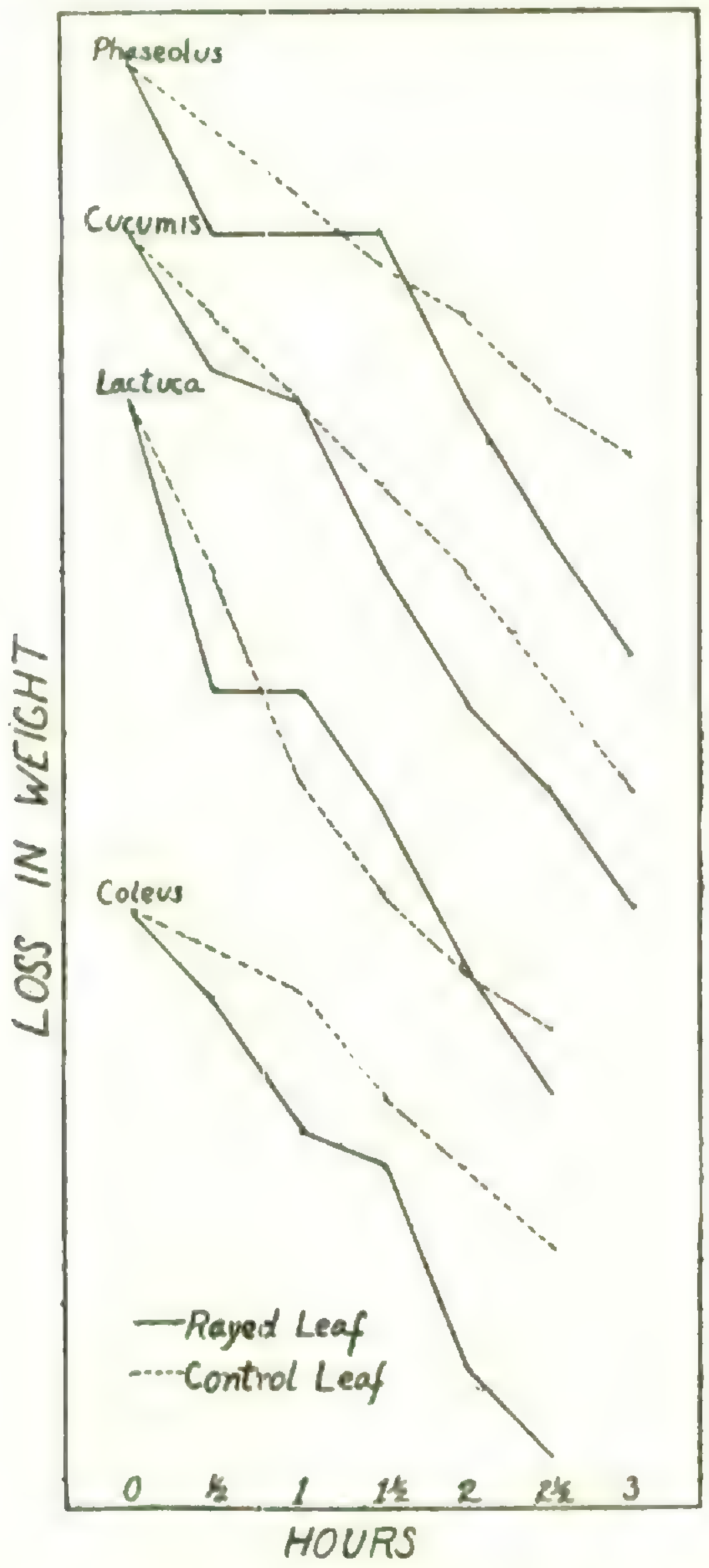

Fig. 2. Showing the comparison between the loss of weight of leaves rayed with an unscreened lamp and those kept in darkness.

TABLE XIII

SHOWING LOSS OF WEIGHT IN GRAMS OF COLEUS LEAVES WITH PARAFFINED STEMS

	Control	Rayed on both sides	Rayed on one side
Original weight	1.90	2.10	1.65
Weight after 12 hours	1.75	1.72	1.20
Loss	.15	.38	.45

Discussion

Several points have been very clearly brought out by the foregoing experiments. All plants rayed with an unscreened

quartz mercury lamp were conspicuously injured. At a distance of 50 inches from such a lamp the injury was very great to all plants. At 100 inches away the injury was not so great for the same length of exposure, probably due to a portion of the injurious rays being absorbed by the atmosphere between the lamp and the plant. It was also evident that at this distance some plants were more resistant to ultra-violet radiation as a whole than others and that younger plants were less resistant than older ones. The latter fact was particularly noticeable in *Lactuca* where the growth of young plants was almost completely stopped while that of older ones was only retarded.

The injury was first evident in the epidermis where many of the cells if not collapsed, forming a false cuticle, were smaller than those of control leaves. After raying for a period of weeks, the injury to newly formed leaves was evident through the entire leaf, causing the mesophyll tissue to be more compact with fewer air-spaces and with little differentiation between the different kinds of cells. In plants such as *Raphanus* the contents of the palisade cells were drawn away from the upper ends of the cells, particularly in regions where the epidermis had collapsed. These results suggest that raying with an unscreened lamp may actually retard growth in individual cells even if it does not kill them.

Bailey ('94), using an open arc lamp, and Kluyver ('11), Ritson and Westbrook (Delf, Ritson and Westbrook, '27), using quartz mercury vapor lamps, obtained similar results though different methods of raying were used in all cases. Bailey and Kluyver found anthocyanin disappearing from rayed *Coleus* leaves when the color was present in the epidermis only.

In the foregoing experiments when *Coleus* was rayed under the same general conditions, the anthocyanin pigment disappeared also from the palisade cells of the leaves and from the entire stem tips.

Until recently the penetration of the short ultra-violet rays was thought to be very slight. In fact a layer of skin was said to inhibit their passage. Macht, Anderson, and Bell ('28), however, using living anesthetized animals have shown that rays as short as 313 $\mu\mu$ penetrate into the peritoneal cavity of a rabbit.

Therefore it might not be unusual for rays to penetrate through plant epidermis into the palisade cells or into the cortex of a stem tip, either destroying the pigment or preventing its formation. Green ('97) has suggested that chlorophyll might act as a screen absorbing injurious rays. This supposition is strengthened by the results of experiments on chlorophyll in this paper where ultra-violet rays were found to have very little, if any, effect upon chlorophyll decomposition. If there is a screening action of chlorophyll, it might not have been evident here due to the small number of chloroplastids present in the cortex of the stem. On the other hand, the rays might not have penetrated deep enough to cause direct action, but may have set up chemical reaction which induced the decomposition of anthocyanin or prevented its formation.

Sheard and Higgins ('27) found that in general rays of 270 to 320 μμ delayed the time of germination and lessened the rate of growth, but that rays of 320–390 μμ were effective in promoting growth.

In the experiments in this paper where the lamp was screened by vita glass which cut out rays below 290 μμ, there were no lesions though the newly formed leaves of *Lactuca*, *Raphanus*, and *Coleus* were thinner. In the other plants used the leaves were either of the same or greater thickness than control leaves.

When the lamp was screened by quartz-lite glass which cut out rays shorter than 310 μμ there was also no evidence of lesions though the same three plants again had thinner leaves, while all others had much thicker leaves than the control plants.

In nearly all cases where leaves were found to be thicker when rayed by a screened lamp, the plants themselves were found to be taller with larger stems and more numerous leaves. In no cases was flower production retarded, and in *Cucumis* and *Phaseolus* it was slightly increased.

Sometimes the increase in size took the form of more numerous and larger air-spaces with only slightly larger cells. This was true of both the stems and leaves of *Cucumis* and *Nicotiana* and of the stems of *Zea Mays*. In other cases there were more air-spaces but when this occurred the palisade cells were very much larger. This was very noticeable in *Ipomoea* and *Phaseolus*. In

the leaves of *Zea Mays* the increased growth was evident only in the form of larger cells.

Coleus plants rayed with a lamp screened by vita glass or quartzlite glass showed a marked increase in growth over control plants, though the thickness of the leaves was inversely proportional to their increase in height and number. This might indicate incipient injury to the leaves with a possible stimulatory effect upon the plant as a whole. In addition there was no loss of red color here as there had been when an unscreened lamp was used.

The results with the use of screens correspond well with those of McCrea ('27), where increased growth was obtained in *Digitalis* by the use of vita glass instead of ordinary glass in a greenhouse, and with those of Tsuji ('18), who produced larger and juicier pineapples by raying them in the field with a weak ultra-violet lamp.

When *Phaseolus* plants with both cotyledons removed were rayed either by a screened or an unscreened lamp there was a retardation in growth compared with corresponding non-rayed plants. When only one cotyledon was removed from *Phaseolus* plants, raying with a screened lamp produced a slight increase in growth over corresponding non-rayed plants. This compares well with the work of Westbrook (Delf, Ritson, and Westbrook, '27) where different lengths of day were used in addition to a short daily raying with an unscreened lamp. In all cases the injury was greater the shorter the day. These results and the fact that older *Lactuca* plants were more resistant than young ones may indicate the possibility that the presence of sufficient food may at least partially overcome the injurious effects of raying.

Clement ('26) found that apples that had been rayed stayed turgid longer than non-rayed ones. Likewise Tsuji ('18) observed that stalks of banana plants that were rayed after being cut kept fresh many days longer than non-rayed ones. The writer has found that if the petioles of *Coleus* leaves were dipped in paraffin and the leaves then rayed with an unscreened lamp first on one side and then on the other for a period of one and a half hours each, they remained turgid at the end of twelve hours, while the control leaves were badly wilted. If, however, the leaves were rayed only on one side the leaves were much more

wilted than the control leaves. All these observations would tend to indicate that a false cuticle is formed wherever plant tissue is rayed heavily with ultra-violet, thus greatly retarding the rate of water loss from the internal tissues.

In the foregoing experiments, using a wide variety of plants in sufficient numbers to avoid individual differences, and using two well-known ultra-violet glasses as screens, the writer has reached the conclusion that increased growth can be obtained in many groups of plants by the daily use of a quartz mercury vapor lamp screened to cut out the harmful short rays. However, results point to the supposition that each variety of plant has its own ultra-violet requirement for best growth and that this can be determined only by experiment.

Summary

1. Raying with an unscreened quartz mercury vapor lamp caused injury in all plants used.

2. Raying with a lamp screened by vita glass was beneficial for some plants, while it produced little visible effect in others. When examined anatomically no lesions were present, but in some cases there was a slight retardation of growth.

3. Raying with a lamp screened by quartz-lite glass injured none and benefited many of the plants. In some cases, however, the benefit was less than when vita glass was used.

4. Except for *Raphanus* and possibly *Lactuca* the healthiest-appearing plants were among those rayed with a screened lamp, although the distance from the light and the screen promoting best growth differed for different plants.

5. Raying with a screened lamp increased flower production slightly.

6. Plants rayed for a period of weeks with an unscreened lamp developed leaves which were thinner than those of corresponding non-rayed plants, the decrease in thickness being due to a partial or complete collapse of the upper epidermal cells, a lack of differentiation of the palisade layer, and a decrease in the number and size of the air-spaces present in the mesophyll tissue.

7. With the exception of *Coleus*, *Raphanus*, and *Lactuca*, leaves of plants rayed with a screened lamp were in general thicker than

corresponding leaves from control plants, though the particular screen and distance from the lamp promoting the formation of the thickest leaves differed for different plants. The increase in thickness was due either to increase in size of cells or to increase in number and size of air-spaces or to both.

8. The stems rayed with a screened lamp were greater in diameter and contained better-developed vascular bundles than non-rayed ones.

9. A limitation of the amount of available food emphasizes the injurious effect of ultra-violet rays.

10. Ultra-violet radiation had very little, if any, effect upon the decomposition of chlorophyll and thus very little effect upon the photosynthetic apparatus.

11. Ultra-violet radiation had no effect upon the P_H of the plants used.

These results again emphasize the fact that each plant has its own ultra-violet requirement for best growth which can be determined only by experiment.

Acknowledgments

The writer wishes to express sincere appreciation to Dr. B. M. Duggar, Professor of Physiological and Applied Botany, University of Wisconsin, formerly Professor of Plant Physiology in the Henry Shaw School of Botany of Washington University, for suggesting this problem and under whose guidance the early part of this work was carried out; to Dr. E. S. Reynolds, Physiologist to the Missouri Botanical Garden, for his advice and helpful criticisms concerning the work; to Dr. C. F. Hagenow, of the Physics Department of Washington University, for spectral photographs; to Dr. LeRoy McMaster, of the Chemistry Department of Washington University, for the use of laboratory and apparatus; and to Dr. G. T. Moore, Director of the Missouri Botanical Garden, for the privileges and facilities of that institution.

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Explanation of Plate

PLATE 21 (SERIES I F, H AND G)

Fig. 1. *Cucumis sativus.*
  A. Plant rayed four weeks at 100 inches from the light without a screen.
  B. Plant not rayed.
Fig. 2. *Cucumis sativus.*
  A. Plant not rayed.
  B. Plant rayed for eight weeks as in fig. 1 A.
Fig. 3. *Raphanus sativus.*
  A. Plants not rayed.
  B. Plants rayed for eight weeks at 100 inches from the light without a screen.
  C. Plants rayed for eight weeks at 50 inches from the light without a screen.
Fig. 4. *Raphanus sativus.*
  A. Plant rayed for eight weeks at 100 inches as in fig. 3 B.
  B. Plant not rayed.
Fig. 5. *Raphanus sativus.*
  A. Plant rayed for four weeks at 100 inches as in fig. 3 B.
  B. Plant not rayed.
Fig. 6. *Ipomoea Batatas.*
  A. Plant rayed for eight weeks at 100 inches from the light without a screen.
  B. Plant not rayed.
Fig. 7. *Raphanus sativus.*
  A. Plant not rayed.
  B. Plant rayed for eight weeks as in fig. 3 B.

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 22 (SERIES I H, F AND G)

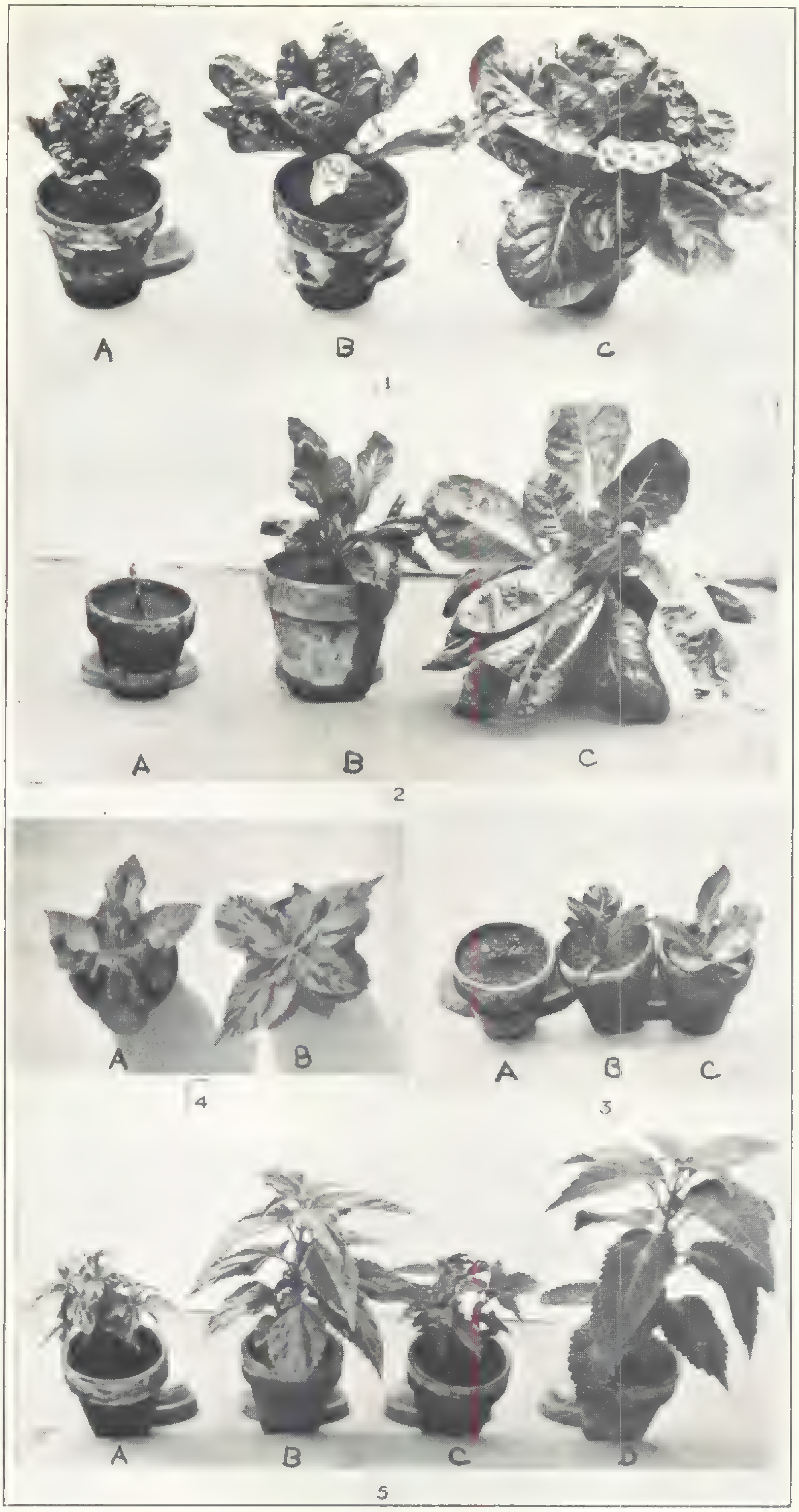
Fig. 1. *Lactuca sativa* (nine leaves) rayed for four weeks.
A. Plant rayed at 50 inches from the light without a screen.
B. Plant rayed at 100 inches from the light without a screen.
C. Plant not rayed.

Fig. 2. *Lactuca sativa* (two leaves) rayed for eight weeks.
A. Plant rayed at 50 inches from the light without a screen.
B. Plant rayed at 100 inches from the light without a screen.
C. Plant not rayed.

Fig. 3. *Lactuca sativa* (two leaves) rayed for four weeks.
A. Plant rayed at 50 inches from the light.
B. Plant rayed at 100 inches from the light without a screen.
C. Plant not rayed.

Fig. 4. *Coleus Blumei* var. "Spotted Gem."
A. Plant rayed for two weeks at 50 inches from the light without a screen.
B. Plant not rayed.

Fig. 5. *Coleus Blumei* vars. *Verschaffeltii* and "Spotted Gem."
A. Var "Spotted Gem" rayed for eight weeks at 100 inches from the light without a screen and then allowed to recover in the greenhouse for four weeks.
B. Var. "Spotted Gem" not rayed.
C. Var. *Verschaffeltii* treated the same as in fig. 5 A.
D. Var. *Verschaffeltii* not rayed.



ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 23 (SERIES I F AND G)

Fig. 1. *Coleus Blumei* vars. "Spotted Gem" and *Verschaffeltii.*

A. Var. "Spotted Gem" rayed for four weeks at 100 inches from the light without a screen.

B. Var. "Spotted Gem" not rayed.

C. Var *Verschaffeltii* rayed under the same conditions as "Spotted Gem."

D. Var. *Verschaffeltii* not rayed.

Fig. 2. *Coleus Blumei* var. "Spotted Gem" and *Verschaffeltii.*

A. Var. *Verschaffeltii* not rayed.

B. Var. *Verschaffeltii* rayed for seven weeks at 100 inches from the light without a screen.

C. Var. "Spotted Gem" rayed for seven weeks under the same conditions as in fig. 2 B.

D. Var. "Spotted Gem" not rayed.

Fig. 3. *Coleus Blumei* var. "Defiance " and "Trailing Queen."

A. Var. "Defiance" not rayed.

B. Var. "Defiance" rayed for four weeks under the same conditions as the plants in fig. 1 A.

C. Var. "Trailing Queen" not rayed.

D. Var. "Trailing Queen" rayed for four weeks under the same conditions as fig. 1 A.

Fig. 4. *Coleus Blumei* var. "Defiance" and "Trailing Queen."

A. Var. "Defiance" not rayed.

B. Var. "Defiance" rayed for seven weeks under the same conditions as fig. 1 A.

C. Var. "Trailing Queen" rayed for seven weeks under the same conditions as fig. 1 A.

D. Var. "Trailing Queen" not rayed.

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

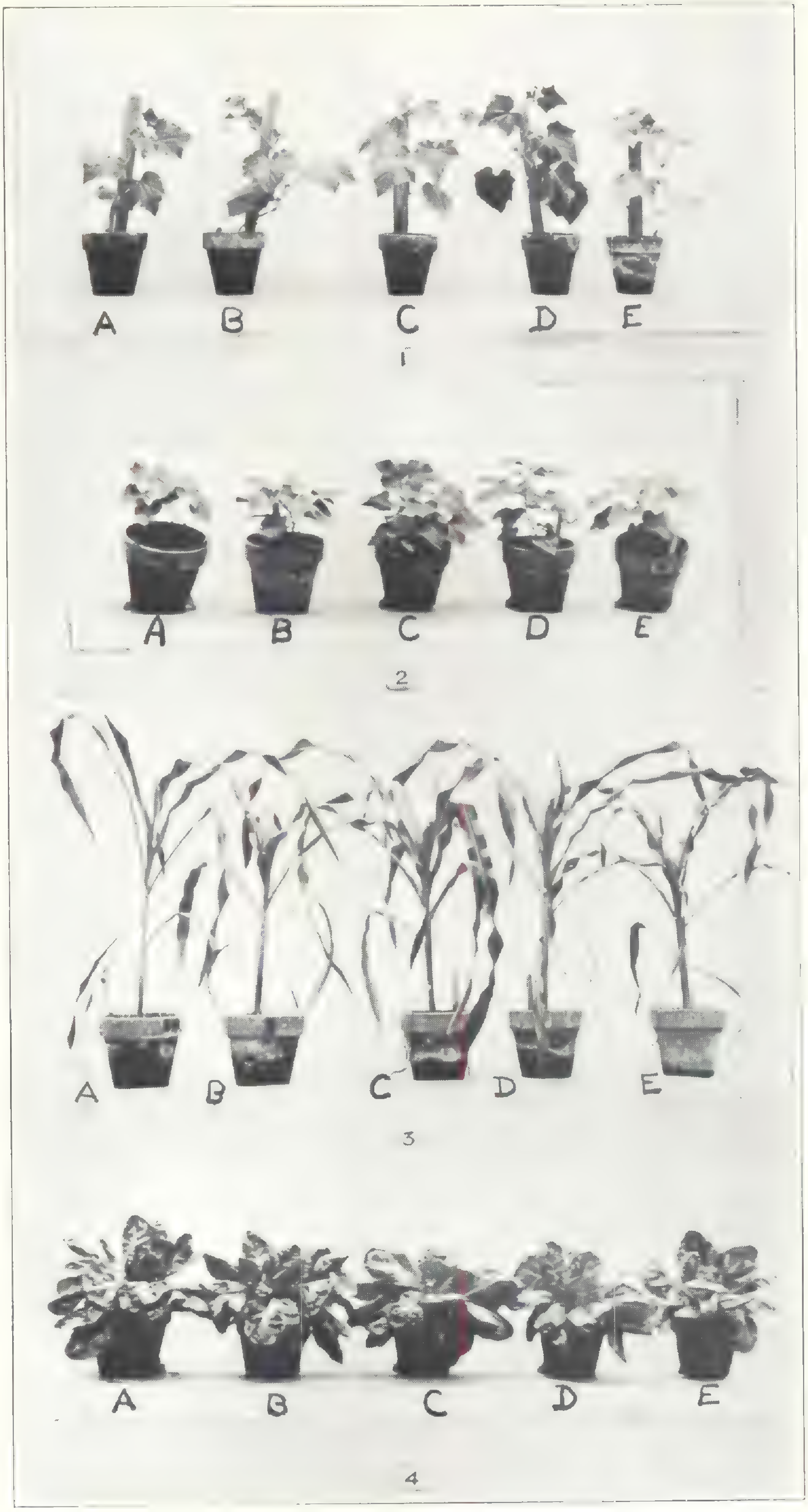
PLATE 24 (SERIES II AND III)

Fig. 1. *Cucumis sativus.*
- A. Plant not rayed.
- B. Plant rayed for seven weeks at 100 inches, using a screen of quartz-lite glass.
- C. Plant rayed for seven weeks at 50 inches, using a screen of quartz-lite glass.
- D. Plant rayed for seven weeks at 100 inches, using a screen of vita glass.
- E. Plant rayed for seven weeks at 50 inches, using a screen of vita glass.

Fig. 2. *Ipomoea Batatas.*
- A. Plant not rayed.
- B. Plant rayed for seven weeks at 100 inches, using a screen of quartz-lite glass.
- C. Plant rayed for seven weeks at 50 inches, using a screen of quartz-lite glass.
- D. Plant rayed for seven weeks at 100 inches, using a screen of vita glass.
- E. Plant rayed for seven weeks at 50 inches, using a screen of vita glass.

Fig. 3. *Zea Mays.*
- A. Plant not rayed.
- B. Plant rayed for seven weeks at 100 inches, using a screen of quartz-lite glass.
- C. Plant rayed for seven weeks at 50 inches, using a screen of quartz-lite glass.
- D. Plant rayed for seven weeks at 100 inches, using a screen of vita glass.
- E. Plant rayed for seven weeks at 50 inches, using a screen of vita glass.

Fig. 4. *Lactuca sativa.*
- A. Plant not rayed.
- B. Plant rayed for seven weeks at 100 inches, using a screen of quartz-lite glass.
- C. Plant rayed for seven weeks at 50 inches, using a screen of quartz-lite glass.
- D. Plant rayed for seven weeks at 100 inches, using a screen of vita glass.
- E. Plant rayed for seven weeks at 50 inches, using a screen of vita glass.



ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 25 (SERIES II AND III)

Fig. 1. *Raphanus sativus.*

A. Plant not rayed.

B. Plant rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

C. Plant rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

D. Plant rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

E. Plant rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

Fig. 2. *Coleus Blumei* var. "Spotted Gem."

A. Plant rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

B. Plant rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

C. Plant rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

D. Plant rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

E. Plant not rayed.

Fig. 3. *Coleus Blumei* var. *Verschaffeltii.*

A. Plant rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

B. Plant rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

C. Plant rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

D. Plant rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

E. Plant not rayed.

Fig. 4. *Bryophyllum pinnatum.*

A. Plant rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

B. Plant rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

C. Plant rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

D. Plant rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

E. Plant not rayed.

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 26

Fig. 1. *Lactuca sativa* (fifteen leaves).
- A. Plant rayed for eight weeks at 100 inches from an unscreened lamp.
- B. Plant not rayed.

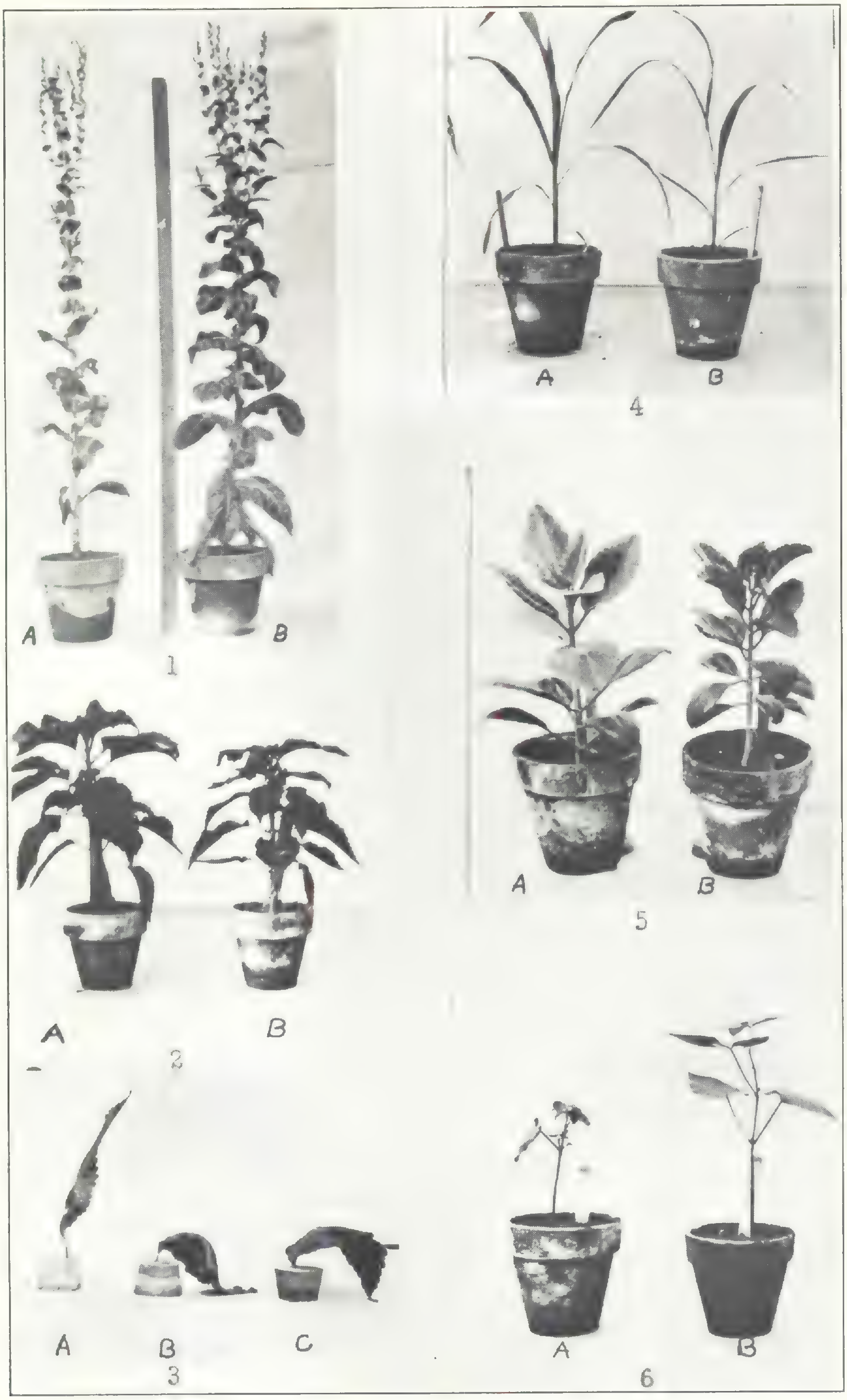
Fig. 2. *Coleus Blumei* var. *Verschaffeltii.*
- A. Plant rayed for thirty seconds each day at 100 inches from an unscreened lamp.
- B. Plant not rayed.

Fig. 3. Leaves of *Coleus Blumei* var. *Verschaffeltii,* with petioles paraffined.
- A. Leaf twelve hours after it had been rayed for 1½ hours on each surface at thirty inches from an unscreened lamp.
- B. Leaf twelve hours after it had been rayed for 1½ hours upon the upper surface at thirty inches from an unscreened lamp.
- C. Unrayed leaf after twelve hours.

Fig. 4. *Zea Mays.*
- A. Plant not rayed.
- B. Plant rayed for six weeks at 100 inches from an unscreened lamp.

Fig. 5. *Bryophyllum pinnatum.*
- A. Plant not rayed.
- B. Plant rayed for six weeks at 100 inches from an unscreened lamp.

Fig. 6. *Phaseolus vulgaris.*
- A. Plant rayed for four weeks at 100 inches from an unscreened lamp.
- B. Plant not rayed.



ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 27

Camera-lucida drawings of equal magnification, using 4-mm. objective and 10 × eyepiece.

Fig. 1. Leaf of *Lactuca sativa* not rayed.

Fig. 2. Leaf of *Lactuca sativa* rayed for four weeks at 100 inches from the light without a screen.

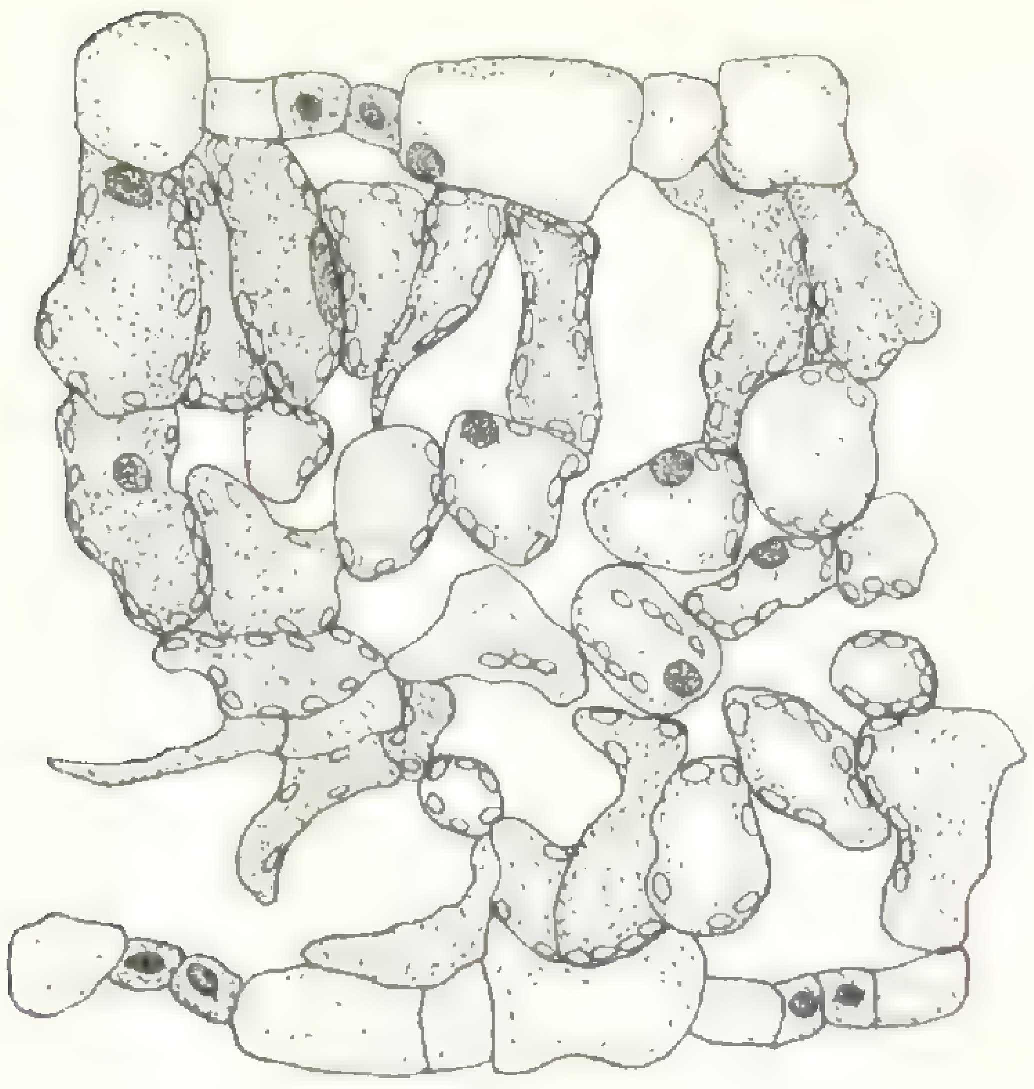
Fig. 3. Leaf of *Lactuca sativa* rayed for eight weeks at 100 inches from the light without a screen.

Fig. 4. Leaf of *Lactuca sativa* rayed for four weeks at 50 inches from the light without a screen.

Fig. 5. Leaf of *Nicotiana Tabacum* rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

Fig. 6. Leaf of *Nicotiana Tabacum* not rayed.

Fig. 7. Leaf of *Nicotiana Tabacum* rayed for four weeks at 50 inches from the light without a screen.



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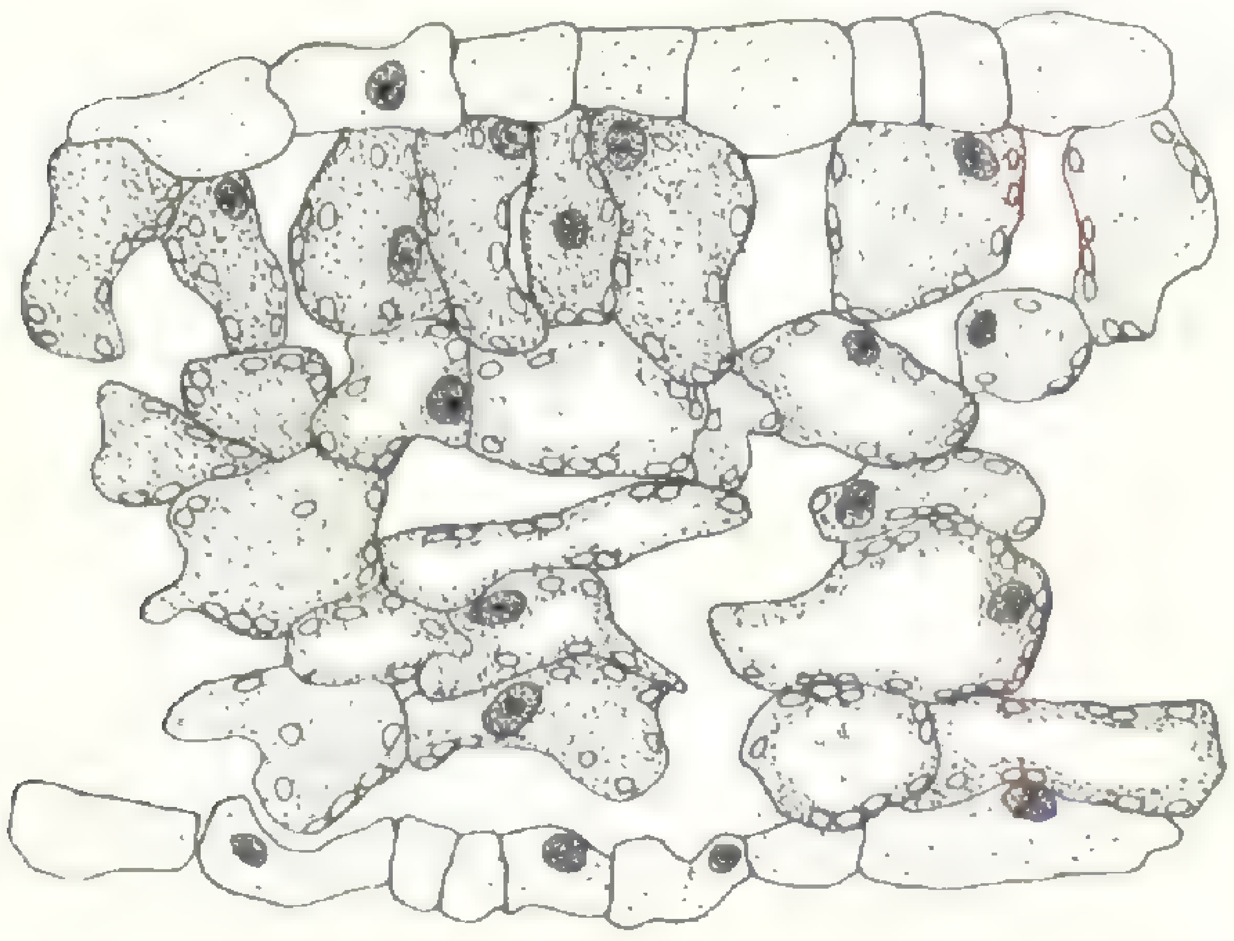

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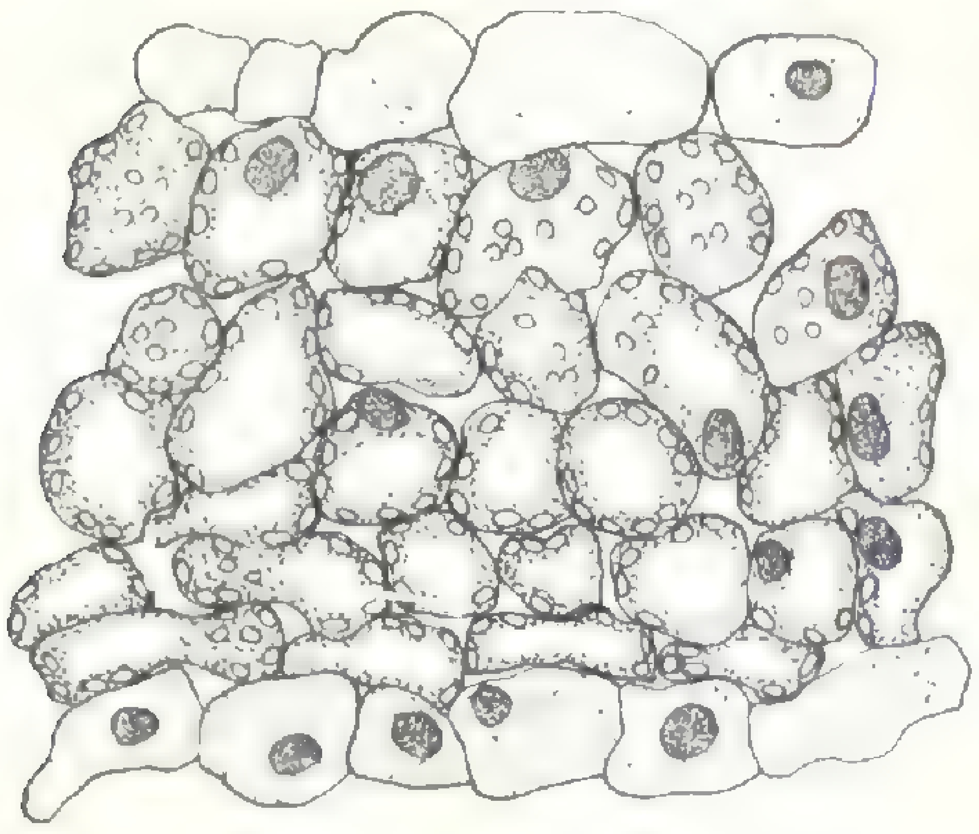

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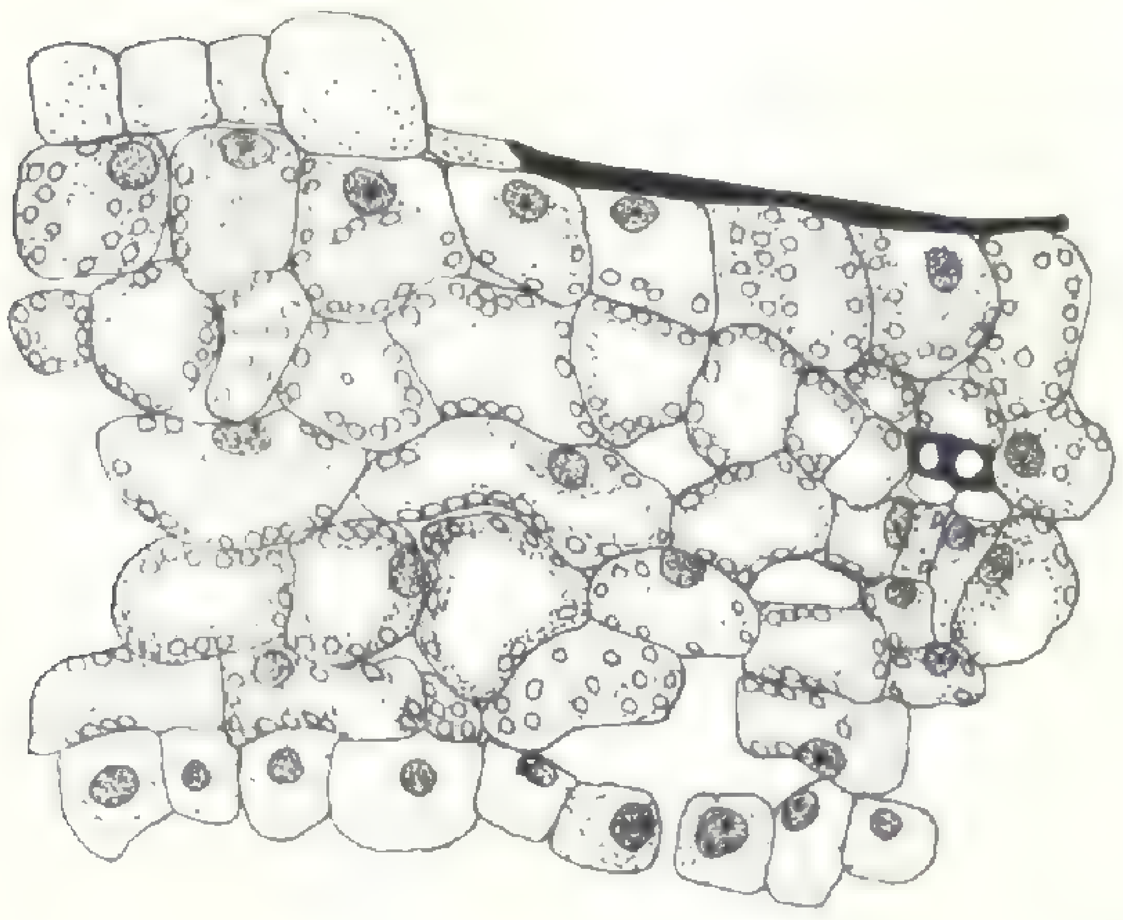

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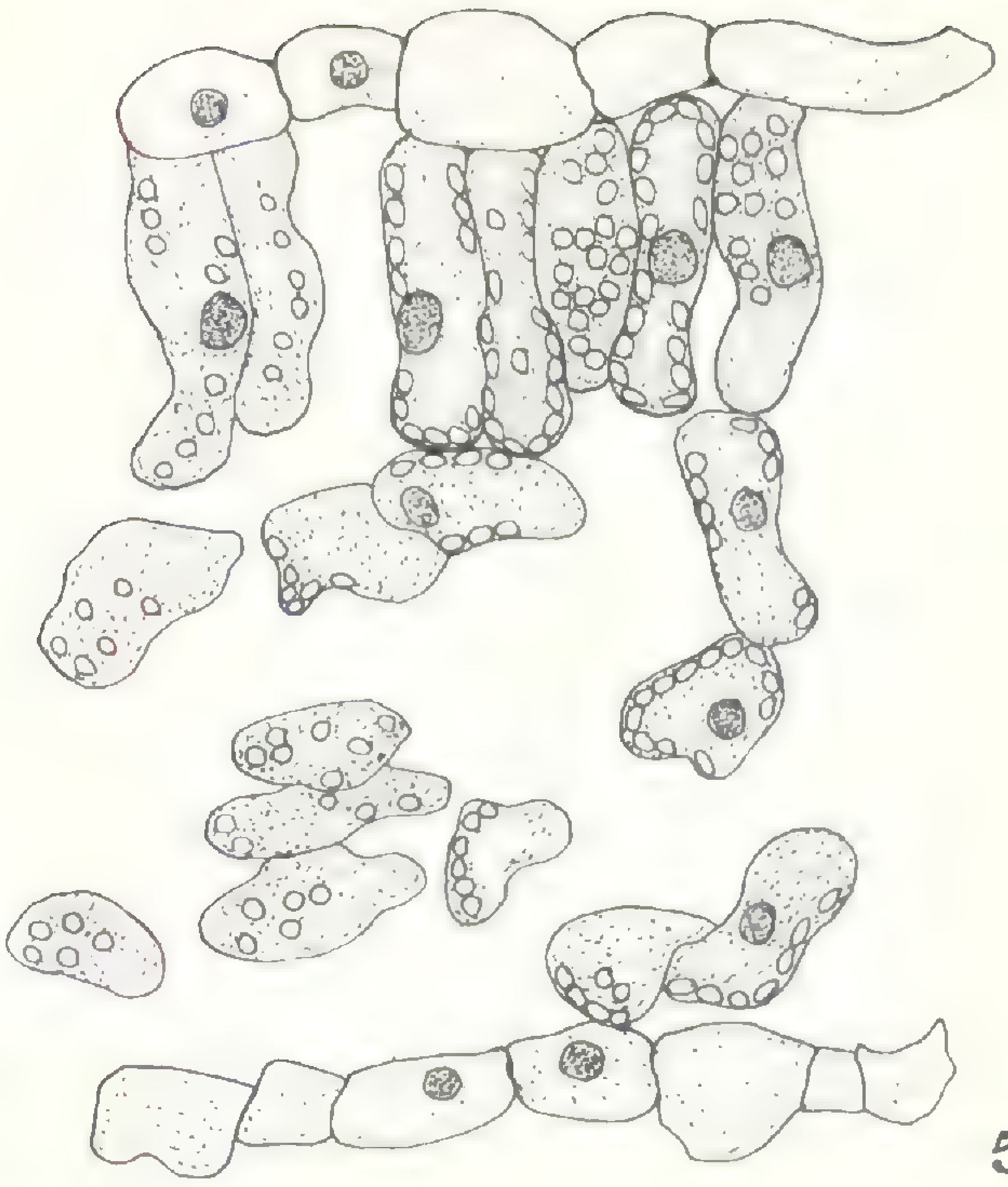

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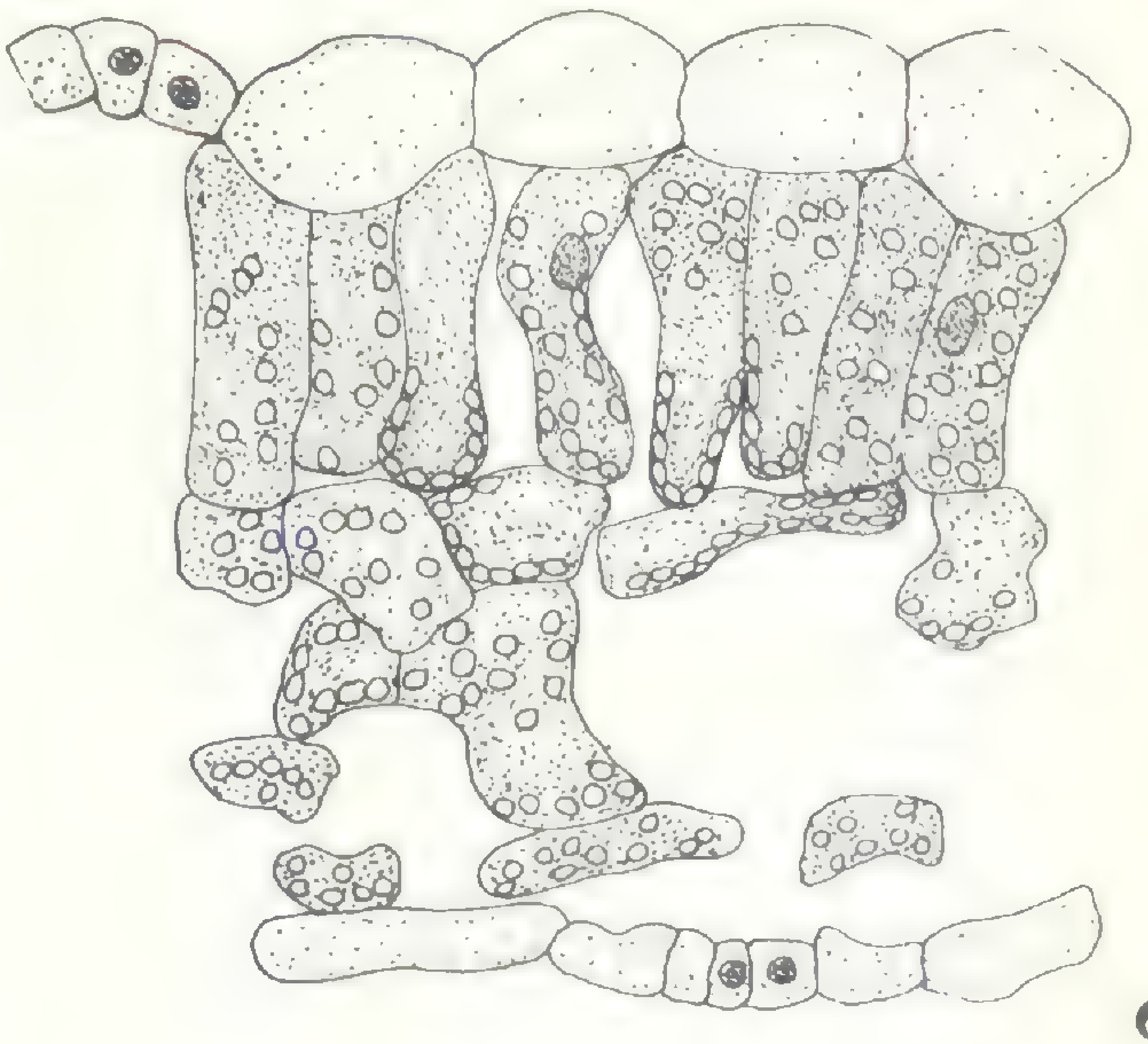

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ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 28

Camera-lucida drawings of equal magnification, using 4-mm. objective and 10 × eyepiece.

Fig. 1. Leaf of *Phaseolus vulgaris* not rayed.

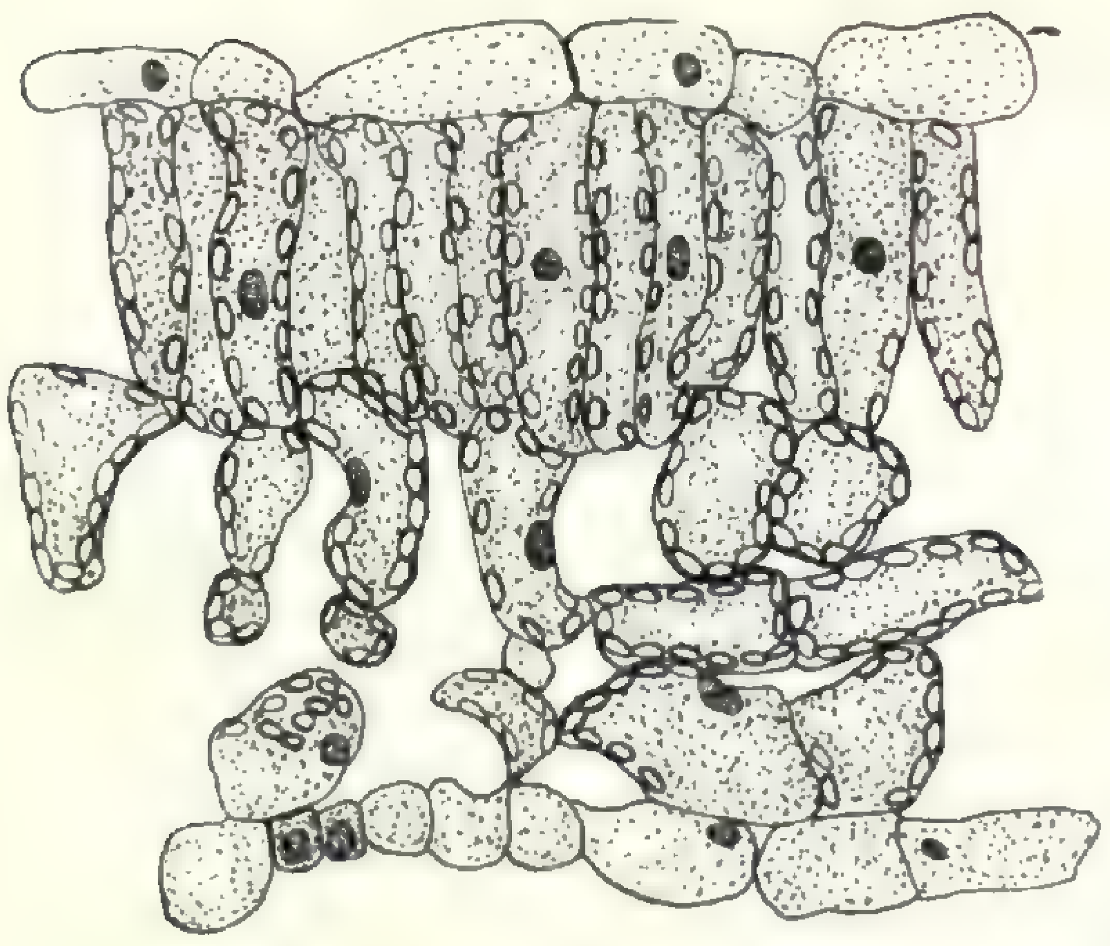
Fig. 2. Leaf of *Phaseolus vulgaris* rayed for four weeks at 100 inches from the light without a screen.

Fig. 3. Leaf of *Phaseolus vulgaris* rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

Fig. 4. Leaf of *Cucumis sativus* not rayed.

Fig. 5. Leaf of *Cucumis sativus* rayed for four weeks at 100 inches from the light without a screen.

Fig. 6. Leaf of *Phaseolus vulgaris* rayed for seven weeks at 50 inches from the light, using a screen of vita glass.



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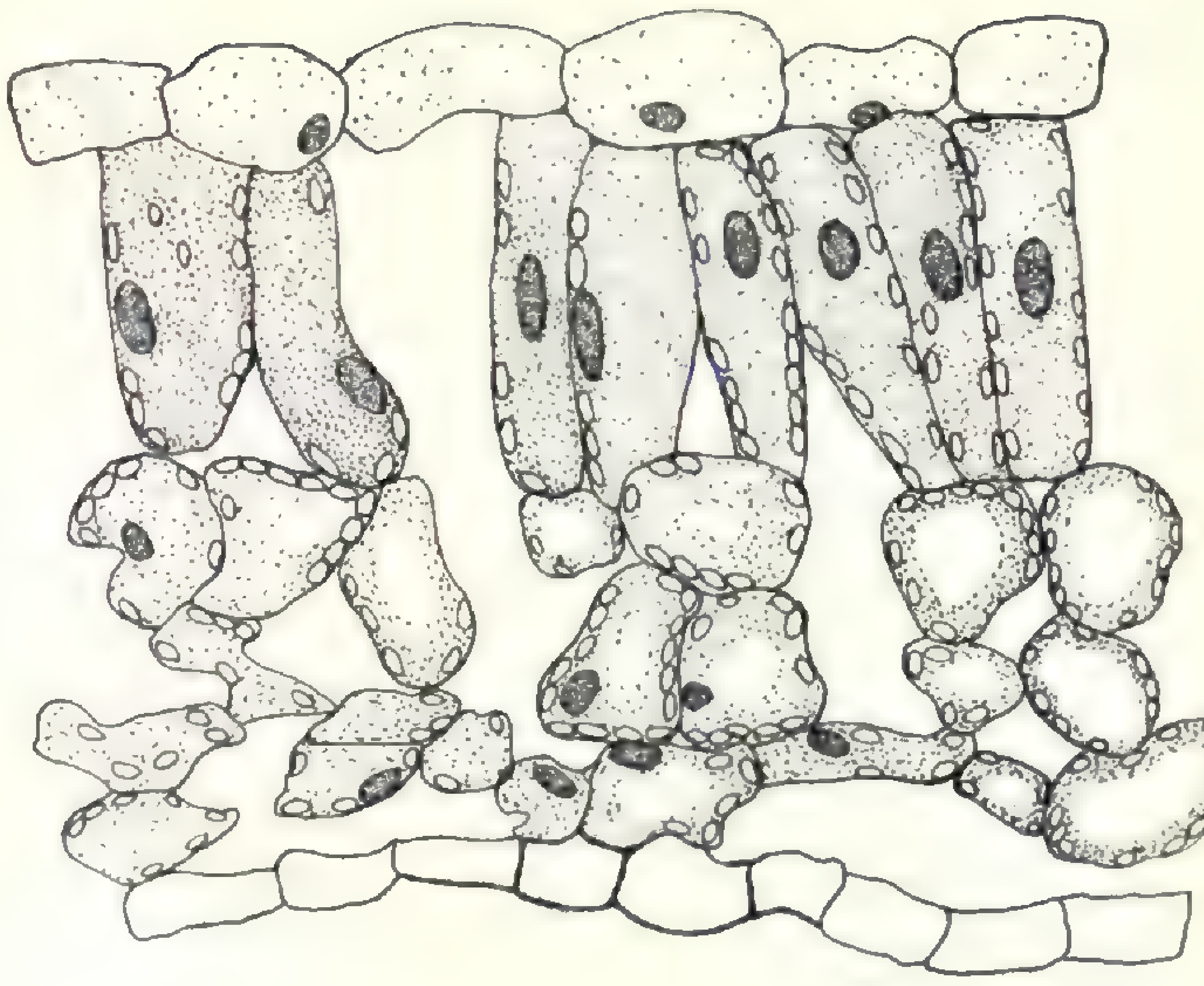

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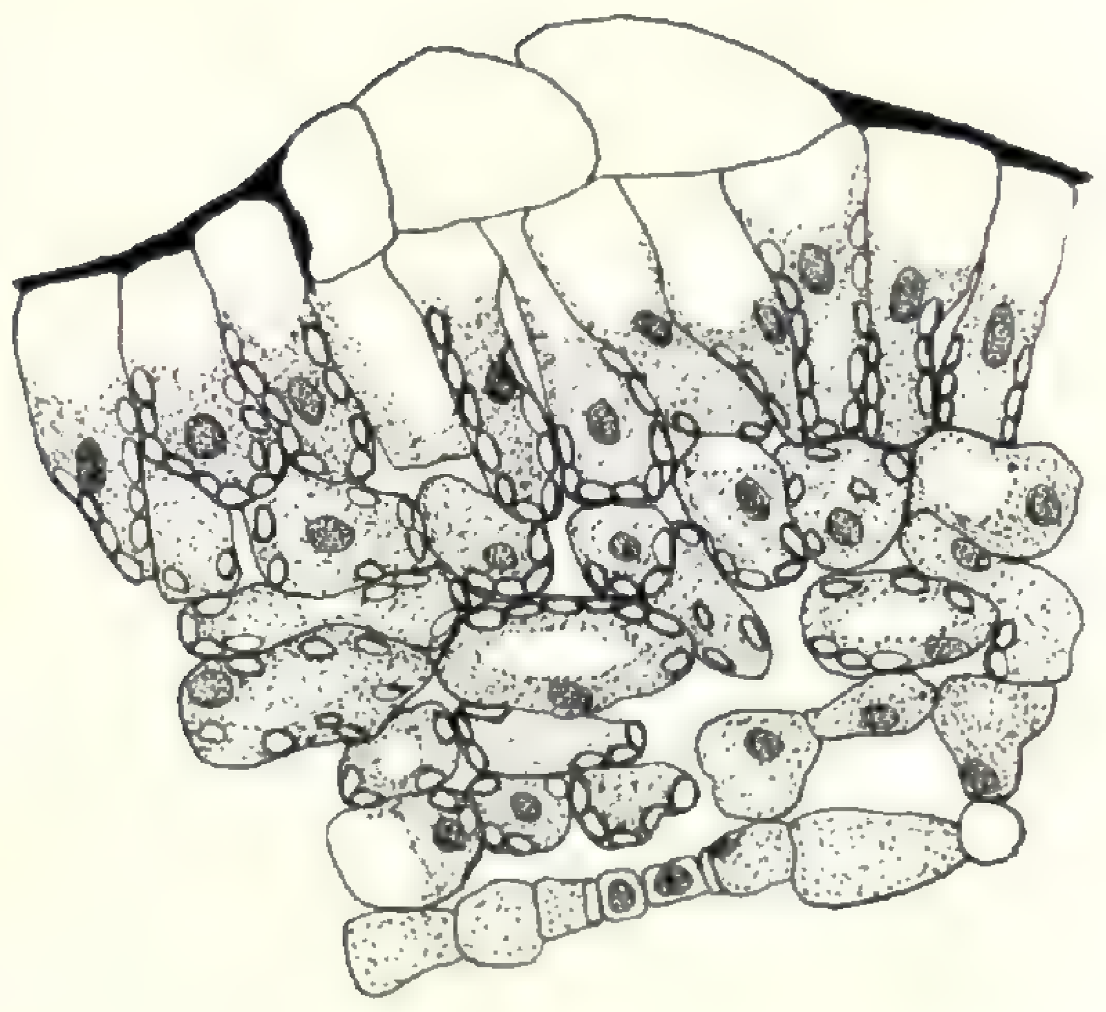

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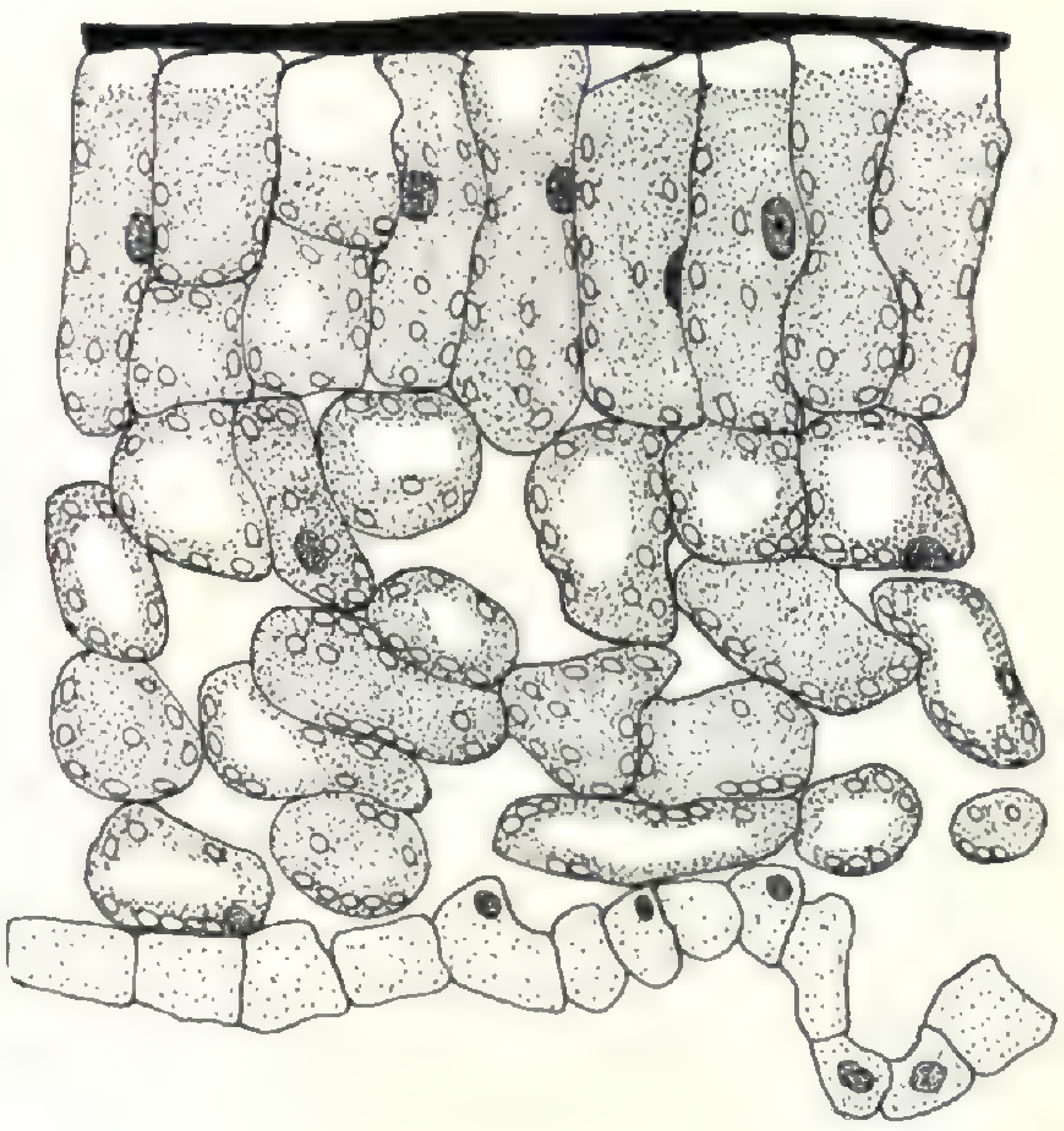

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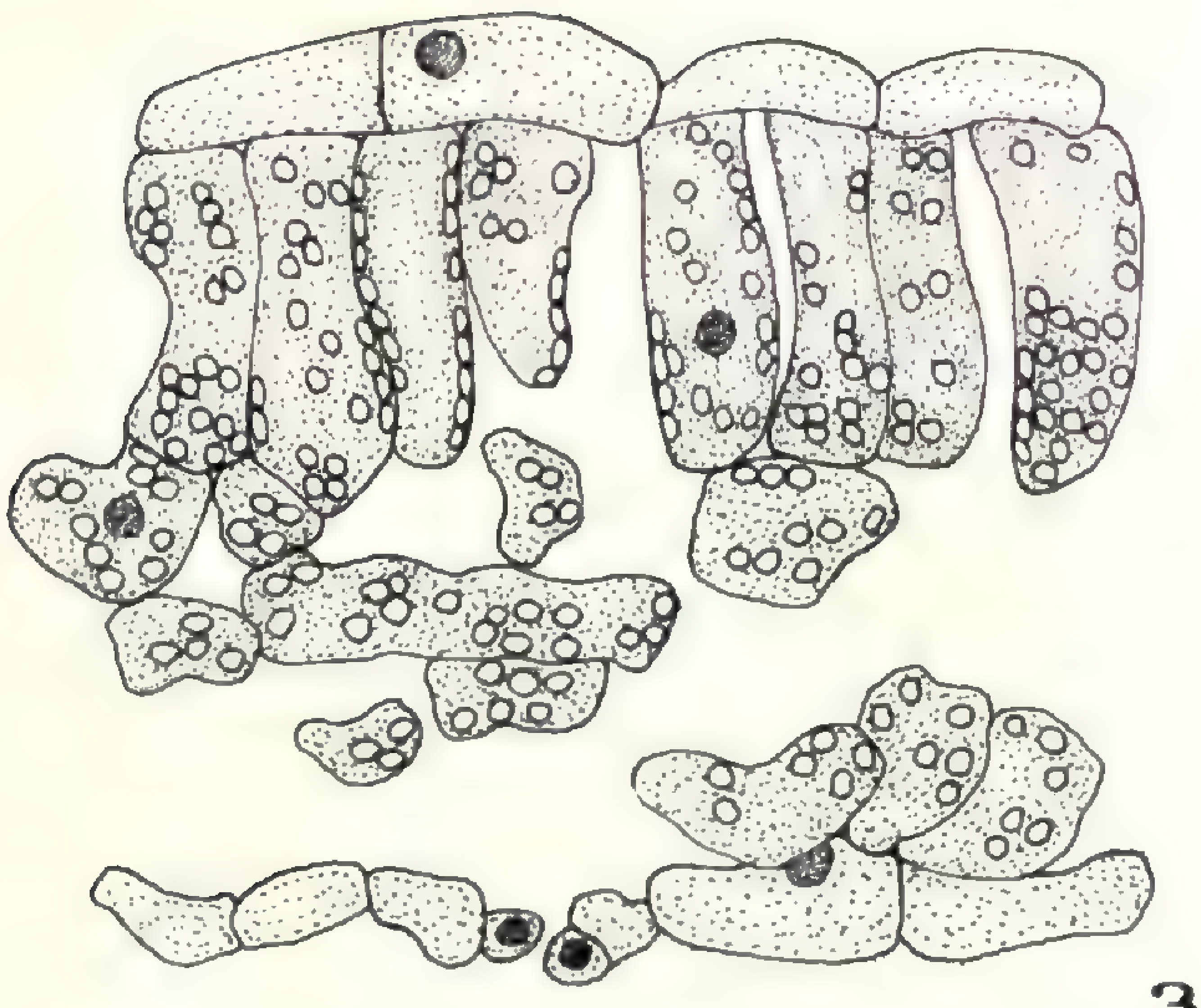

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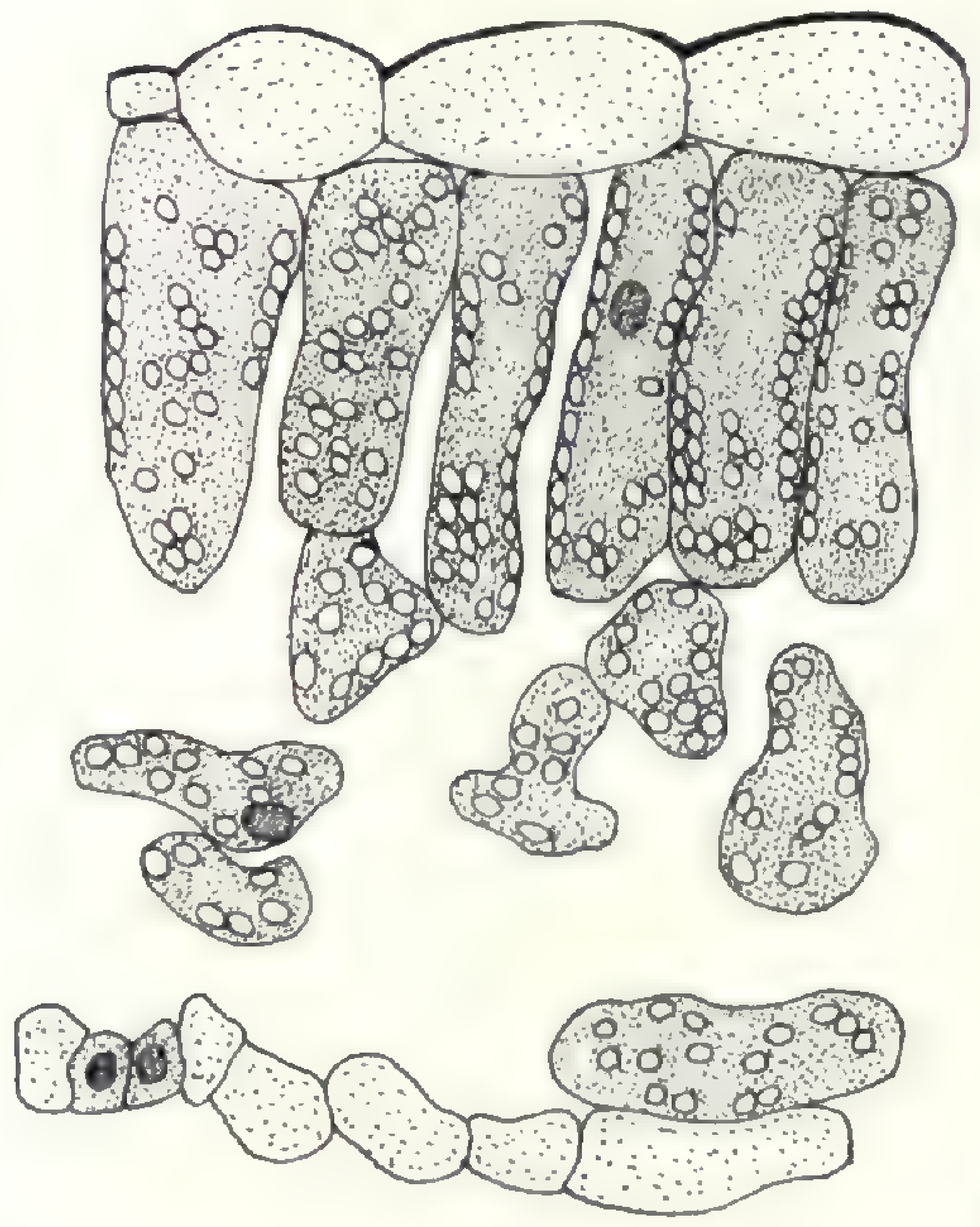


6

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 29

Camera-lucida drawings of equal magnification, using 4-mm. objective and 10 × eyepiece.

Fig. 1. Leaf of *Cucumis sativus* unrayed.

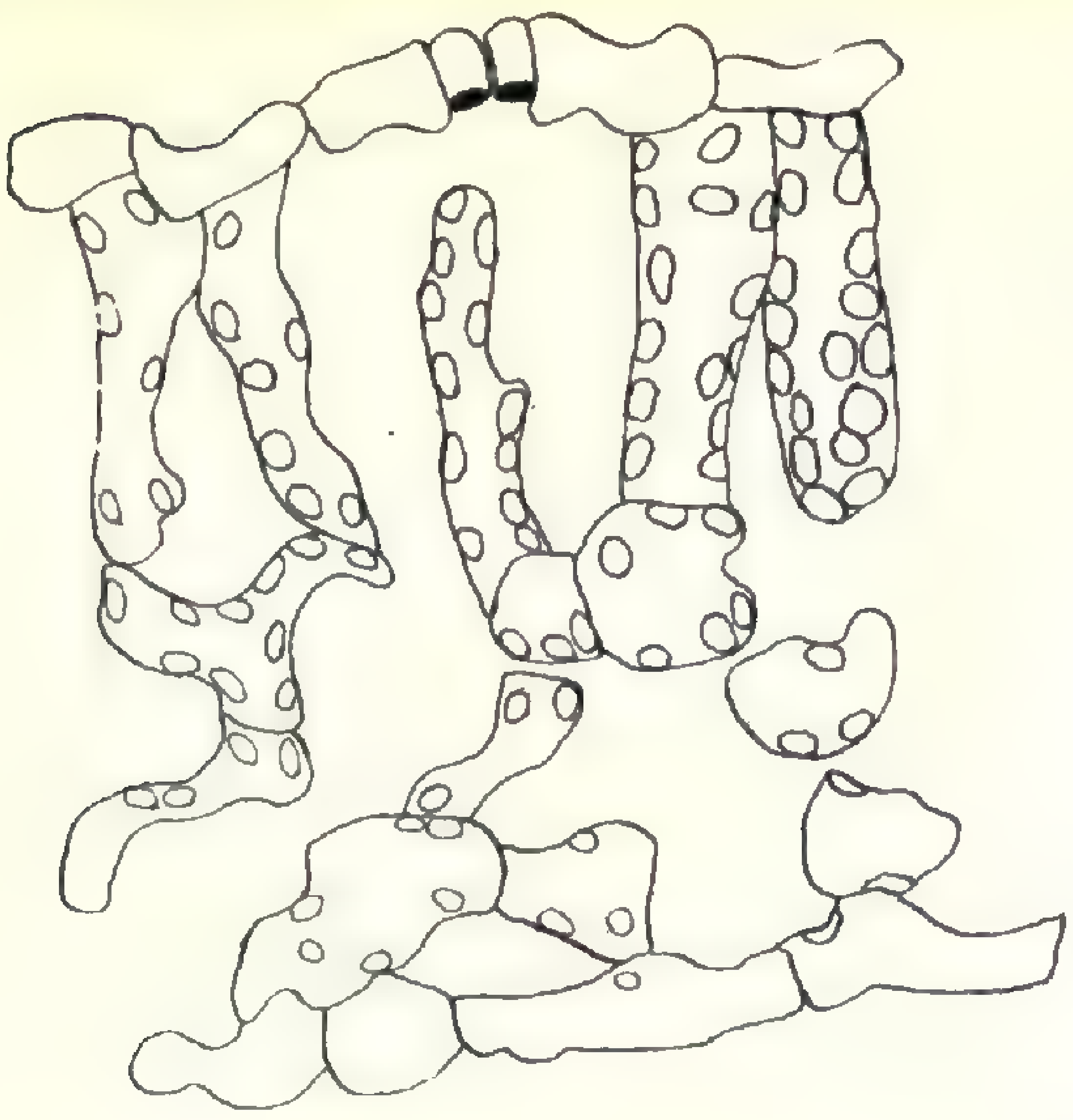
Fig. 2. Leaf of *Cucumis sativus* rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

Fig. 3. Leaf of *Cucumis sativus* rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

Fig. 4. Leaf of *Ipomoea Batatas* unrayed.

Fig. 5. Leaf of *Ipomoea Batatas* rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

Fig. 6. Leaf of *Ipomoea Batatas* rayed at 50 inches from the light without a screen.



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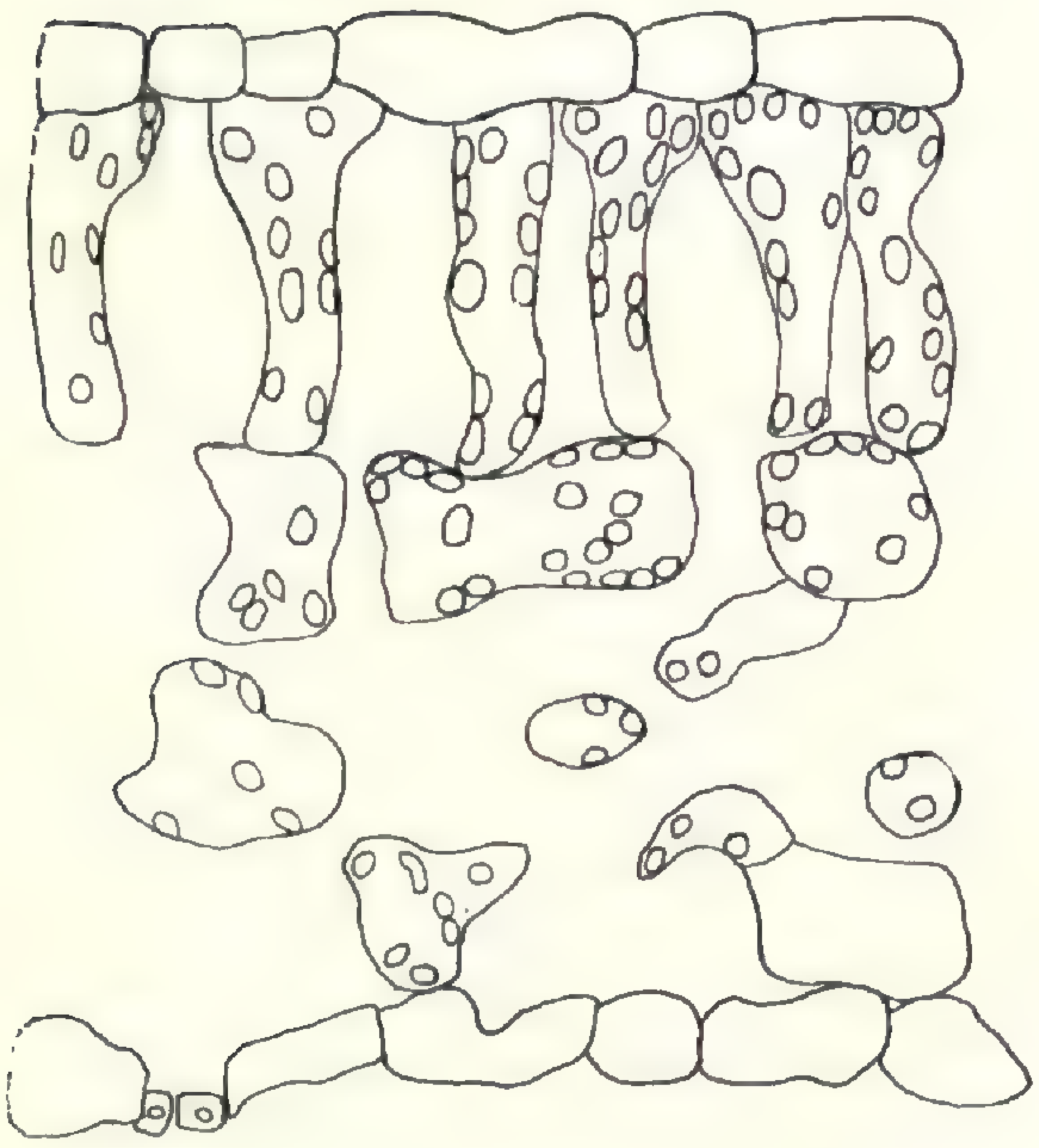

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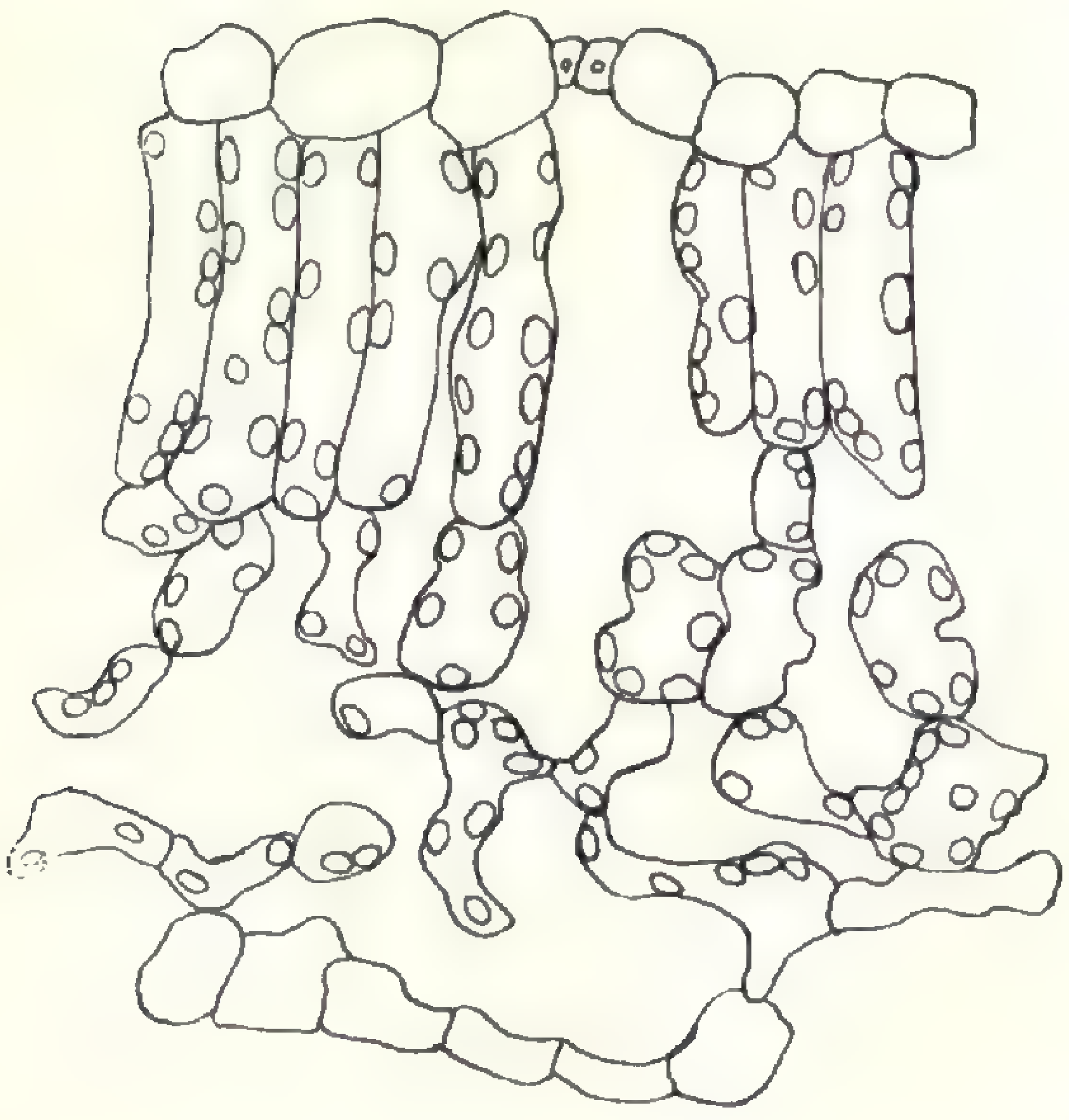

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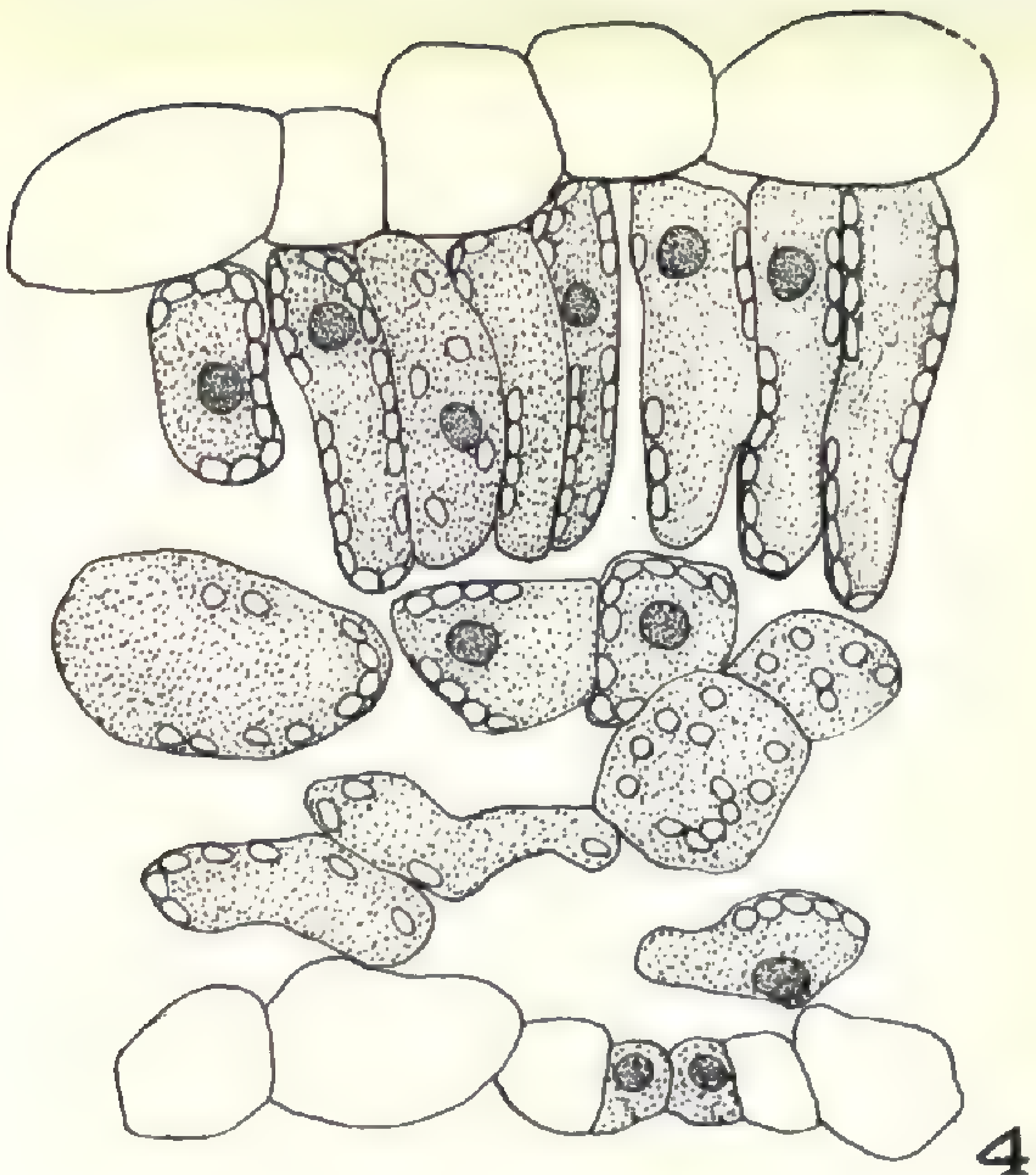

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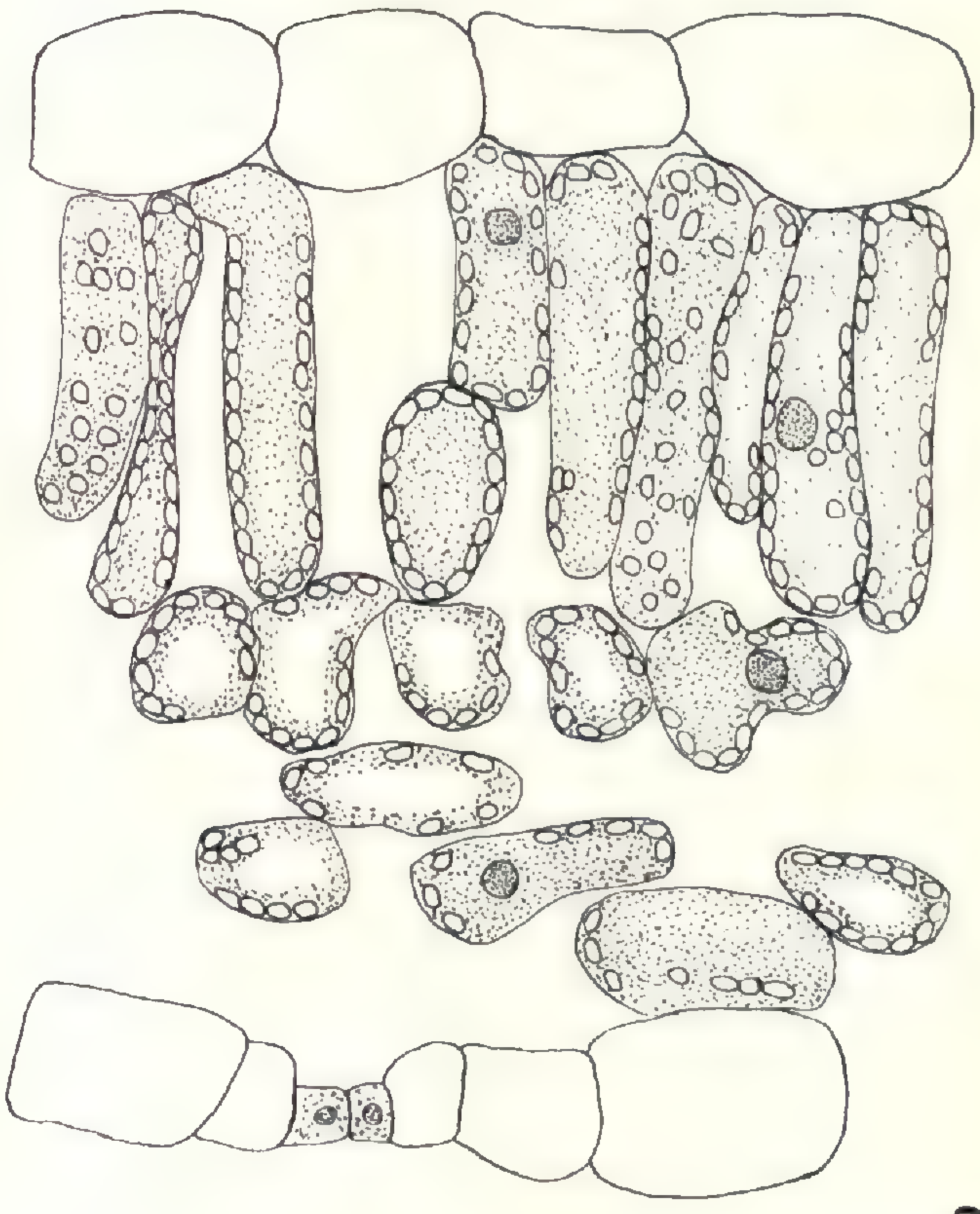

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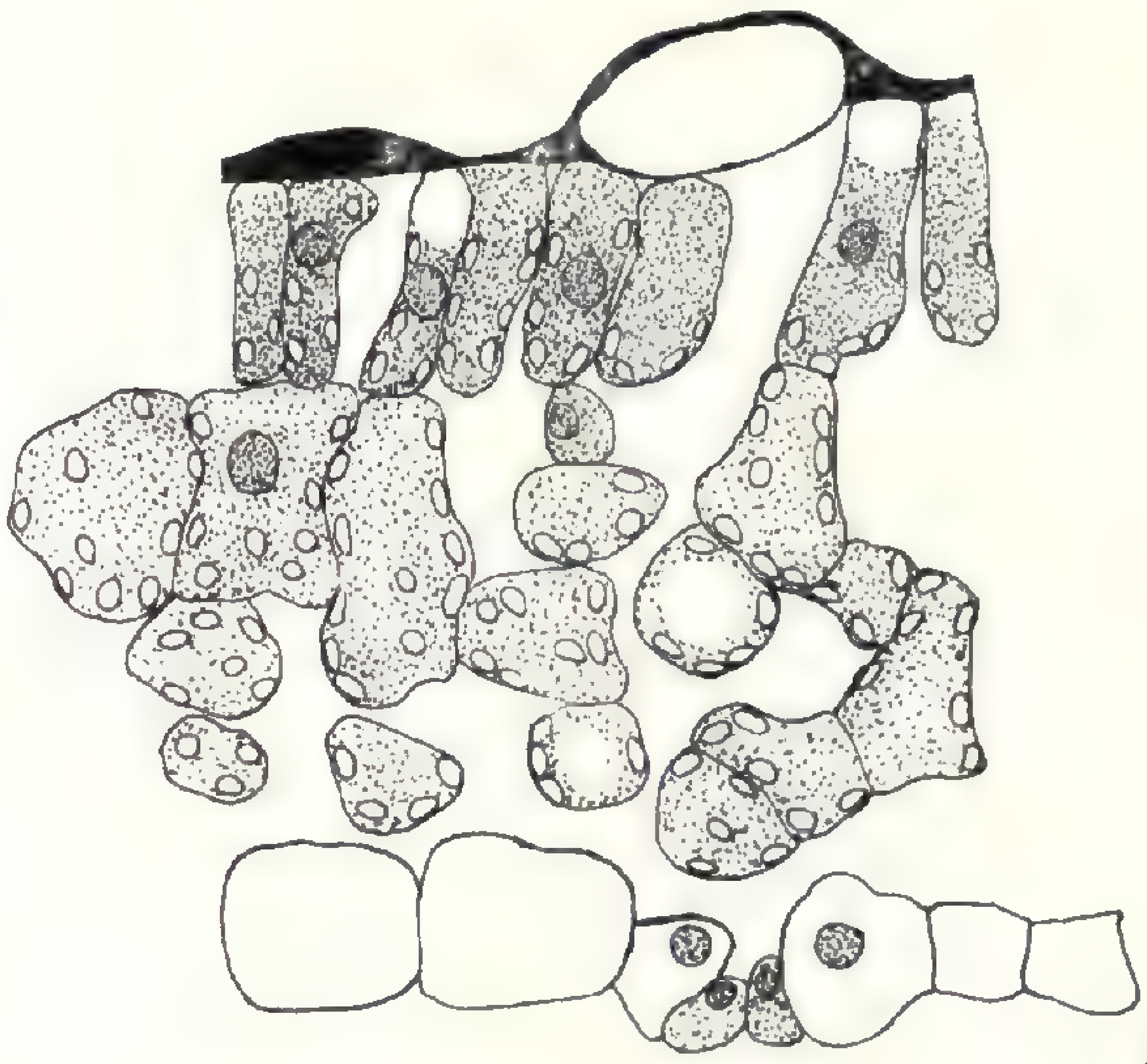


6

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 30

Camera-lucida drawings of equal magnification, using 4-mm. objective and 10 × eyepiece.

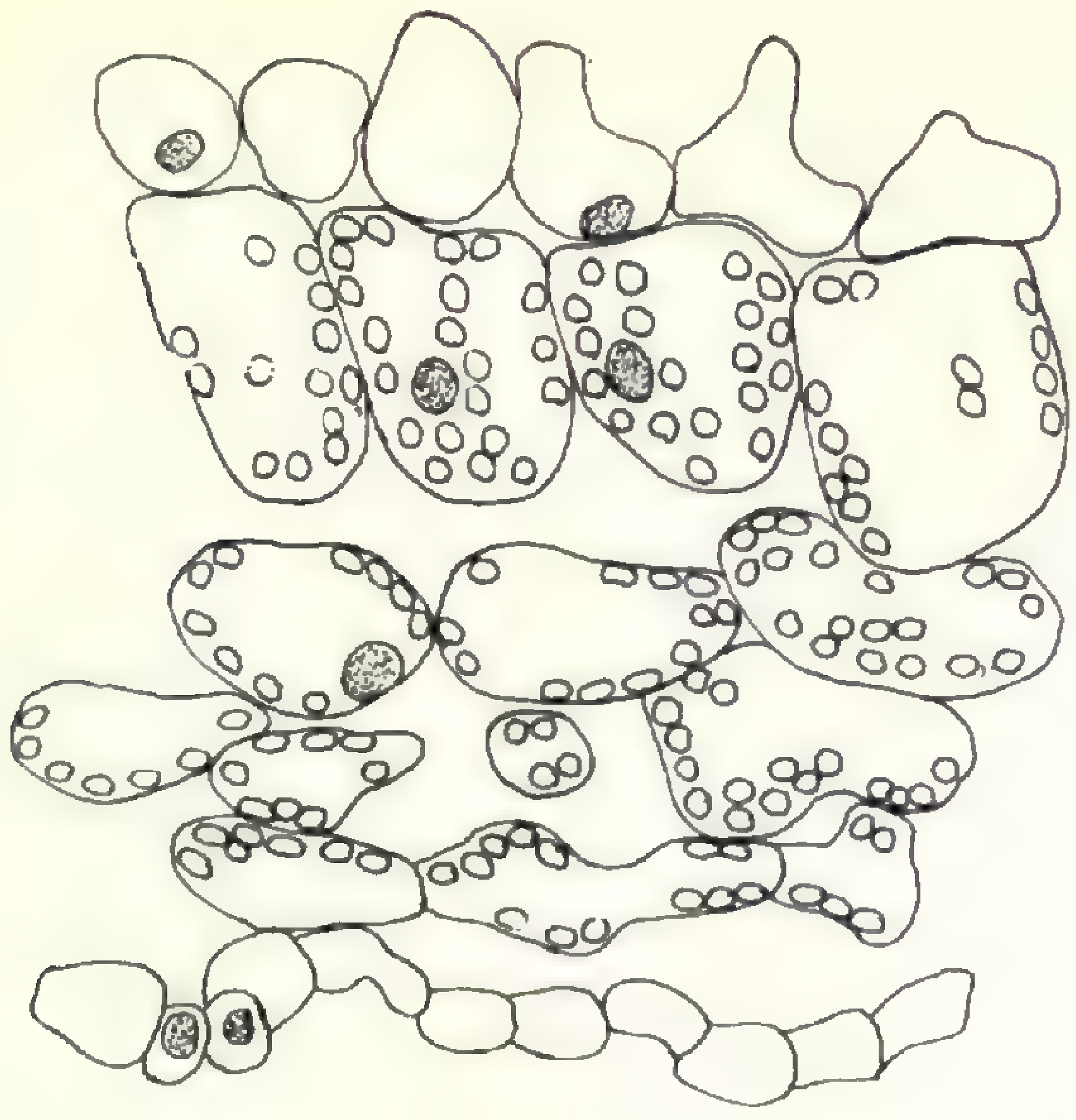
Fig. 1. Leaf of *Coleus Blumei* var. *Verschaffeltii* rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

Fig. 2. Leaf of *Coleus Blumei* var. *Verschaffeltii* rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

Fig. 3. Leaf of *Coleus Blumei* var. *Verschaffeltii* not rayed.

Fig. 4. Leaf of *Coleus Blumei* var. *Verschaffeltii* rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

Fig. 5. Leaf of *Coleus Blumei* var. *Verschaffeltii* rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.



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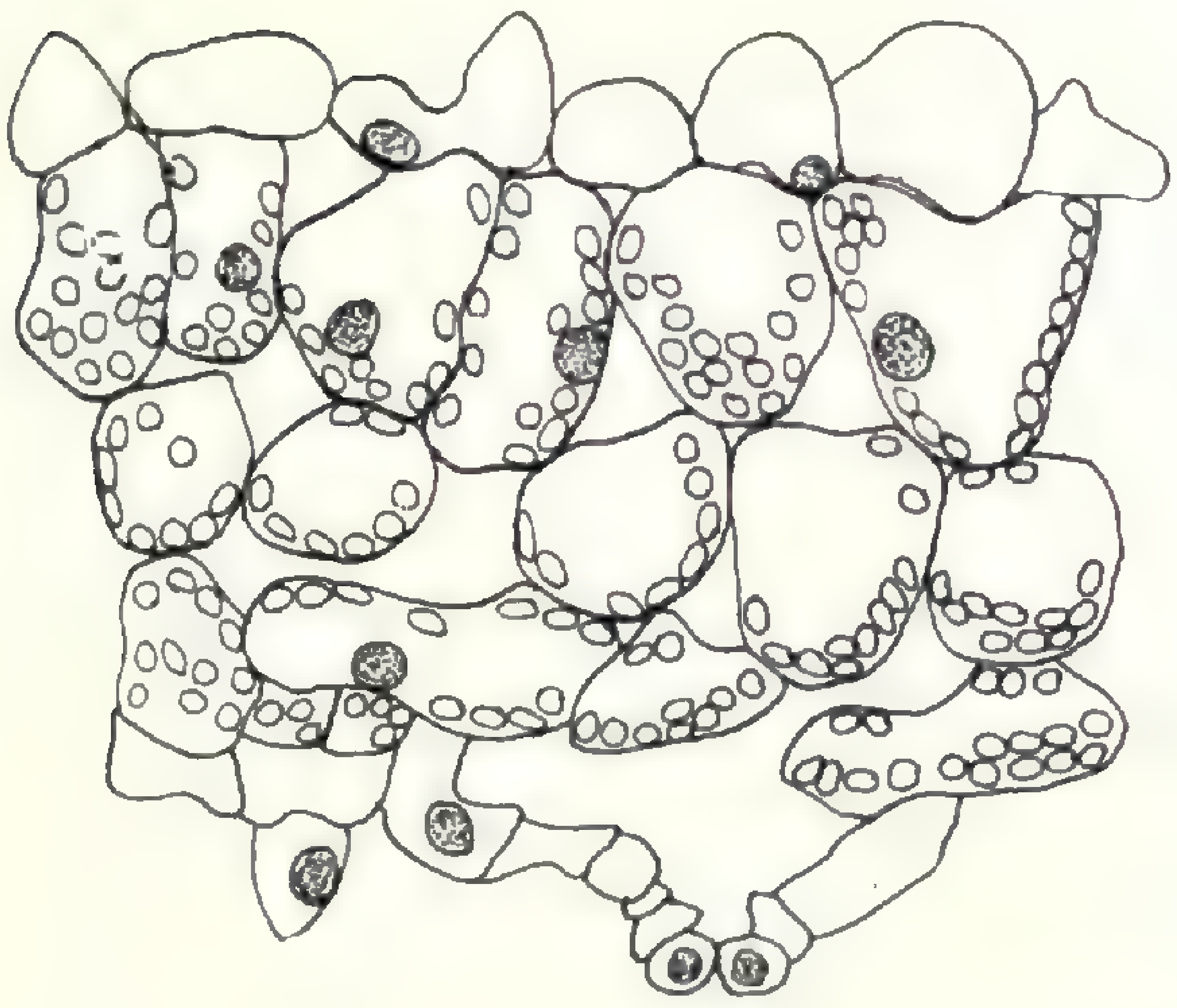

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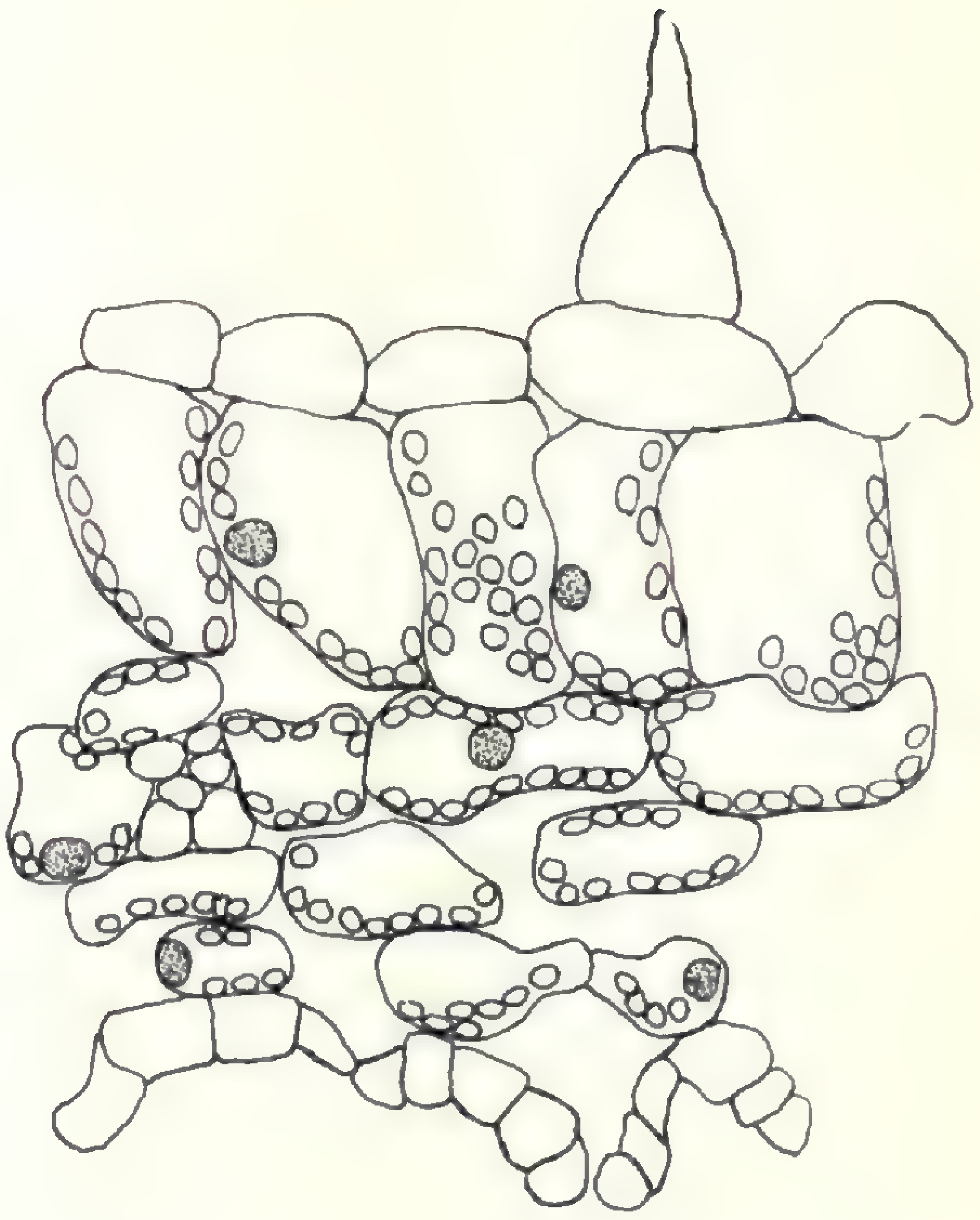

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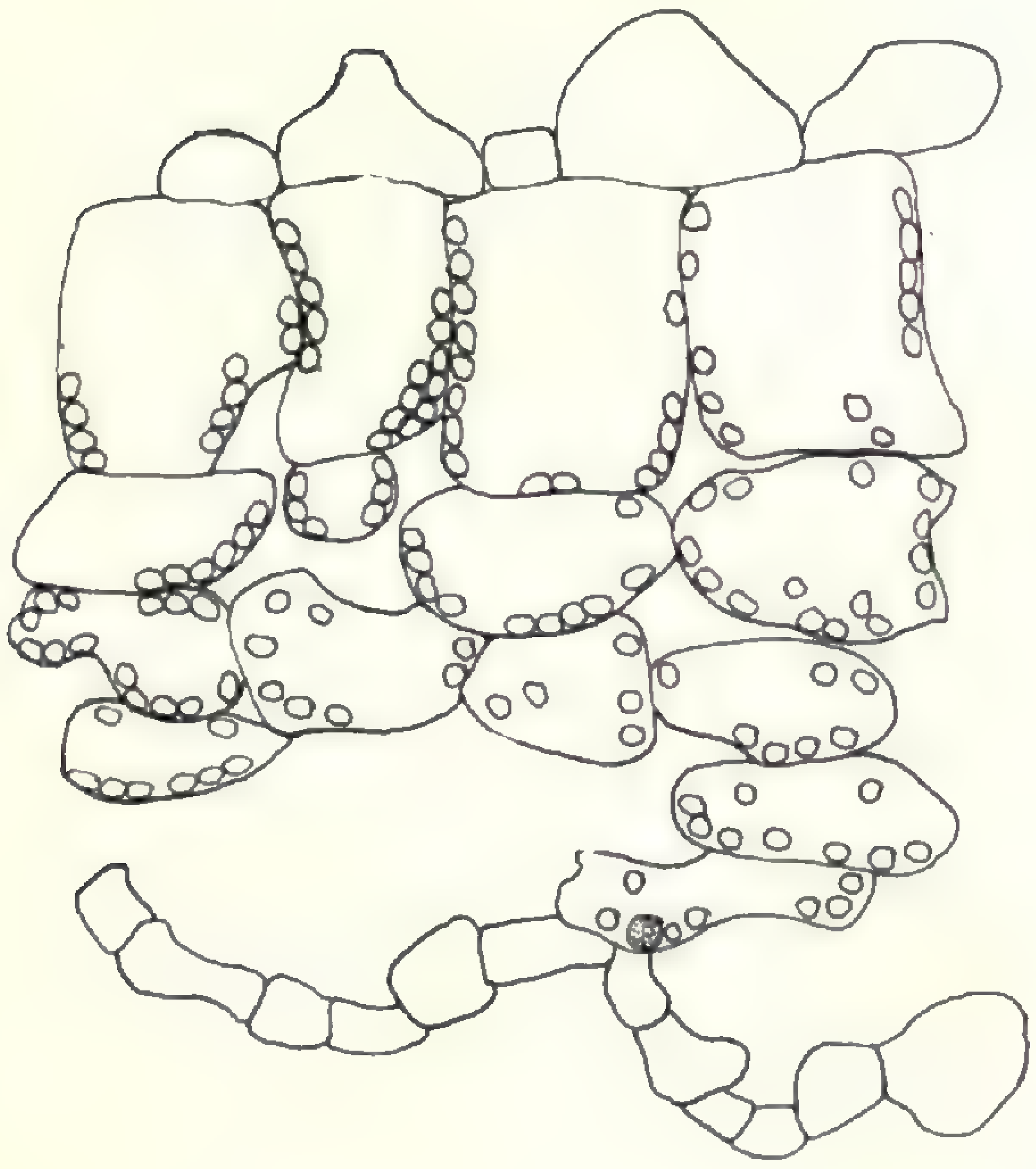

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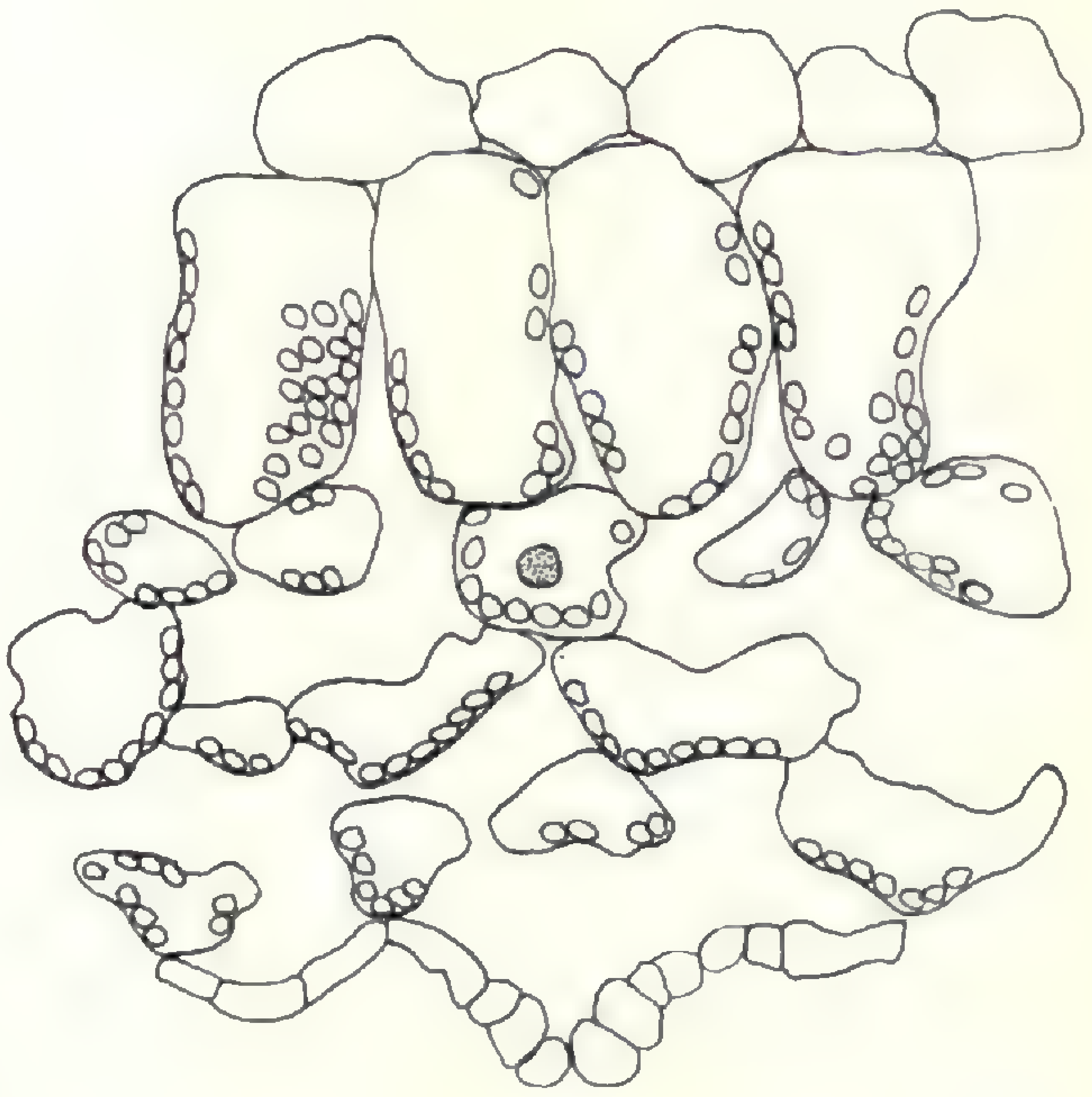


5

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 31

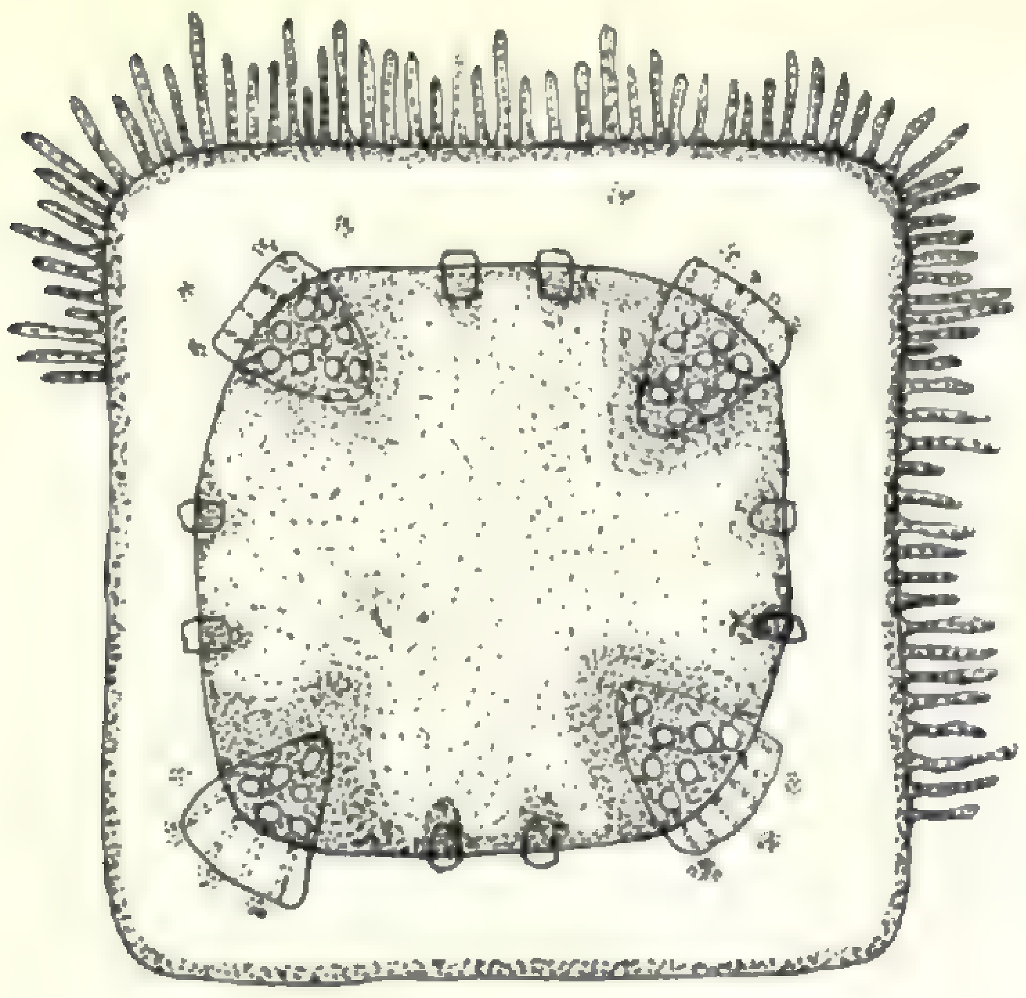
Fig. 1. Diagram of the cross-section of a stem of *Coleus Blumei*, the stippling indicating the normal distribution of red color.

Fig. 2. Diagram of the cross-section of a stem of *Coleus Blumei*, showing the distribution of red color at the end of the fifth raying at 50 inches from the light without a screen.

Fig. 3. Diagram of the cross-section of a stem of *Coleus Blumei*, showing the distribution of red color at the end of the tenth raying at 50 inches from the light without a screen.

Fig. 4. Cross-section of a leaf of *Coleus Blumei*, showing normal distribution of red color.

Fig. 5. Cross-section of a leaf of *Coleus Blumei*, showing the distribution of red color after ten rayings at 50 inches from the light without a screen. Drawn to the same scale as fig. 4.



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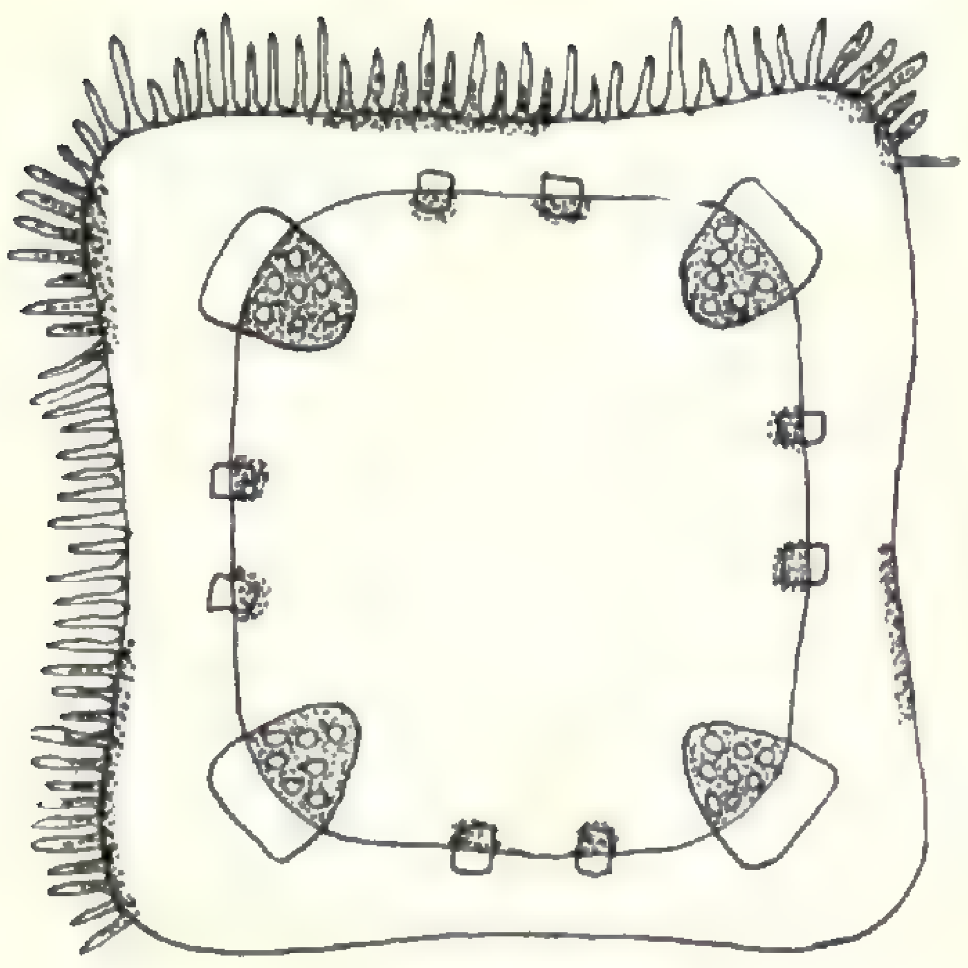

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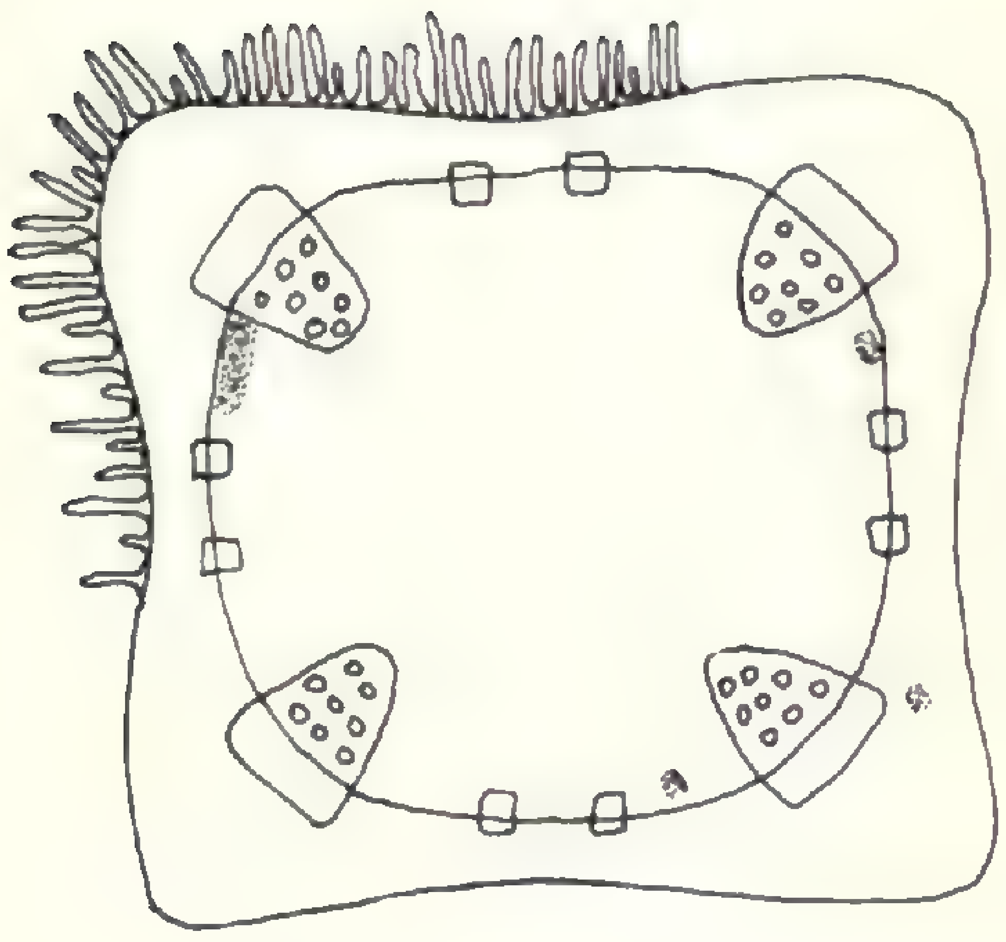

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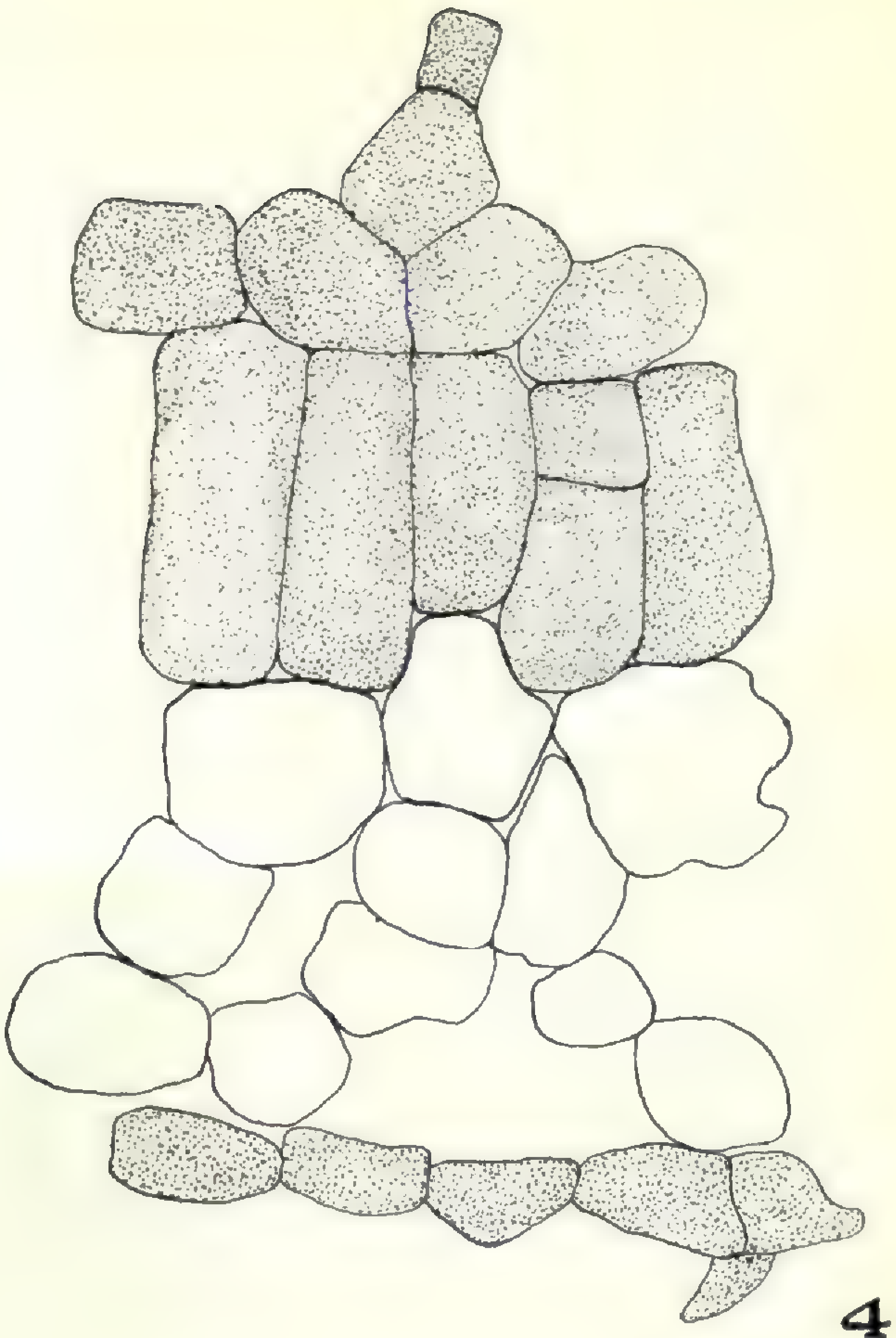

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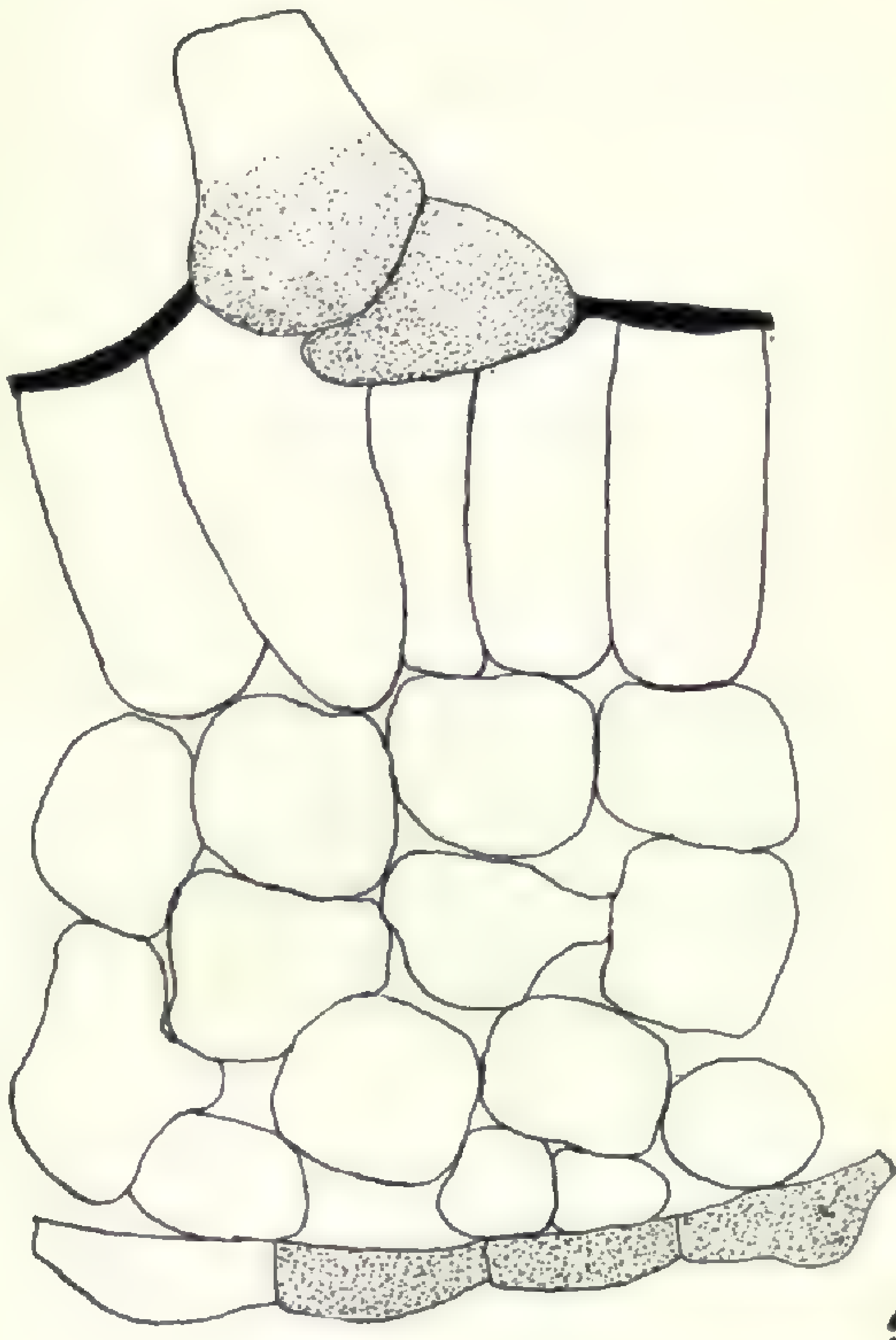


5

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 32

Camera-lucida drawings of equal magnification, using a 4-mm. objective and 10 × eyepiece.

Fig. 1. Leaf of *Zea Mays* unrayed.

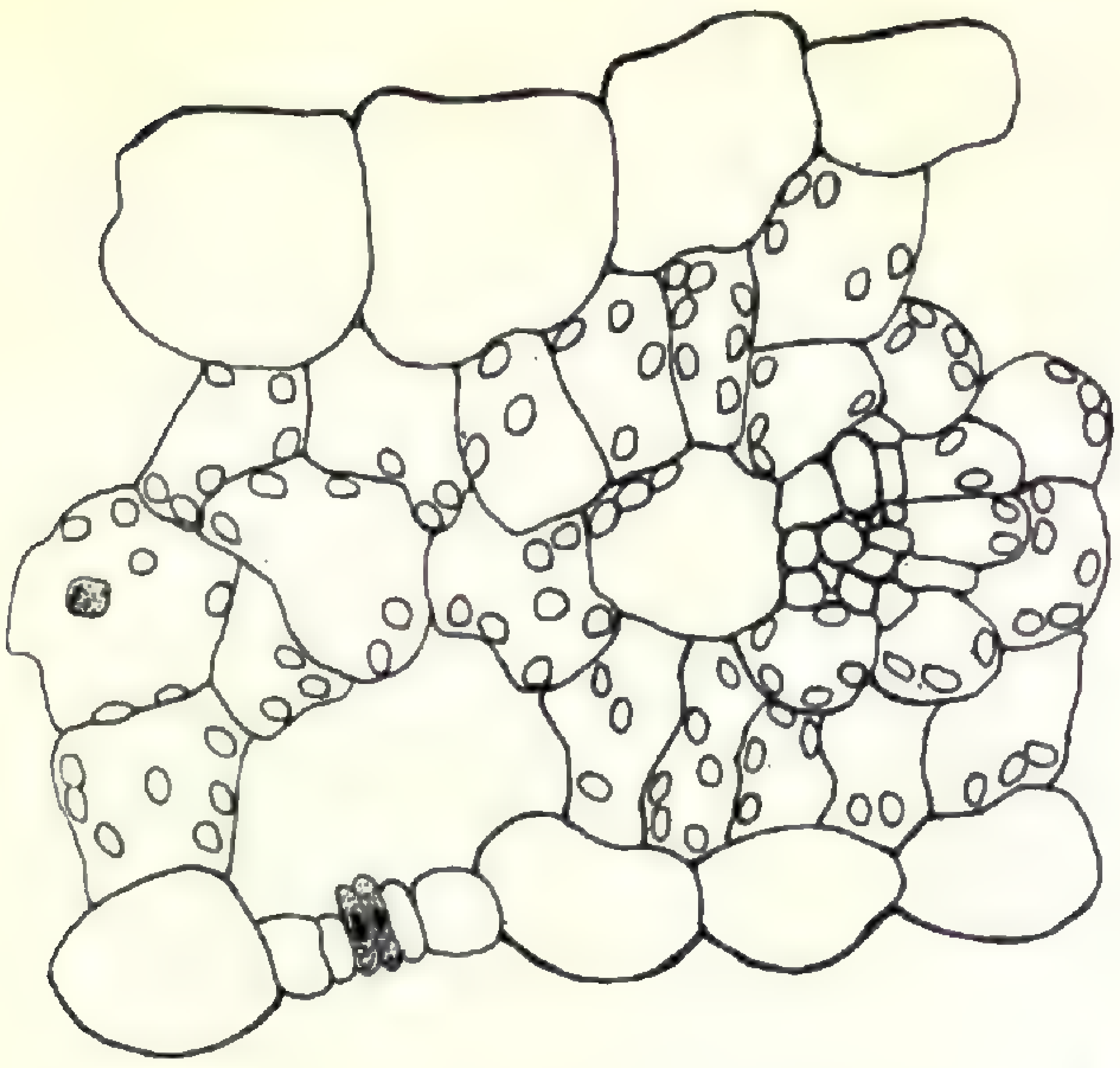
Fig. 2. Leaf of *Zea Mays* rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

Fig. 3. Leaf of *Zea Mays* rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

Fig. 4. Leaf of *Zea Mays* rayed for seven weeks at 100 inches from the light, using a screen of quartz-lite glass.

Fig. 5. Leaf of *Zea Mays* rayed at 100 inches from the light for seven weeks, using a screen of vita glass.

Fig. 6. Leaf of *Zea Mays* rayed for seven weeks at 100 inches from the light, using no screen.



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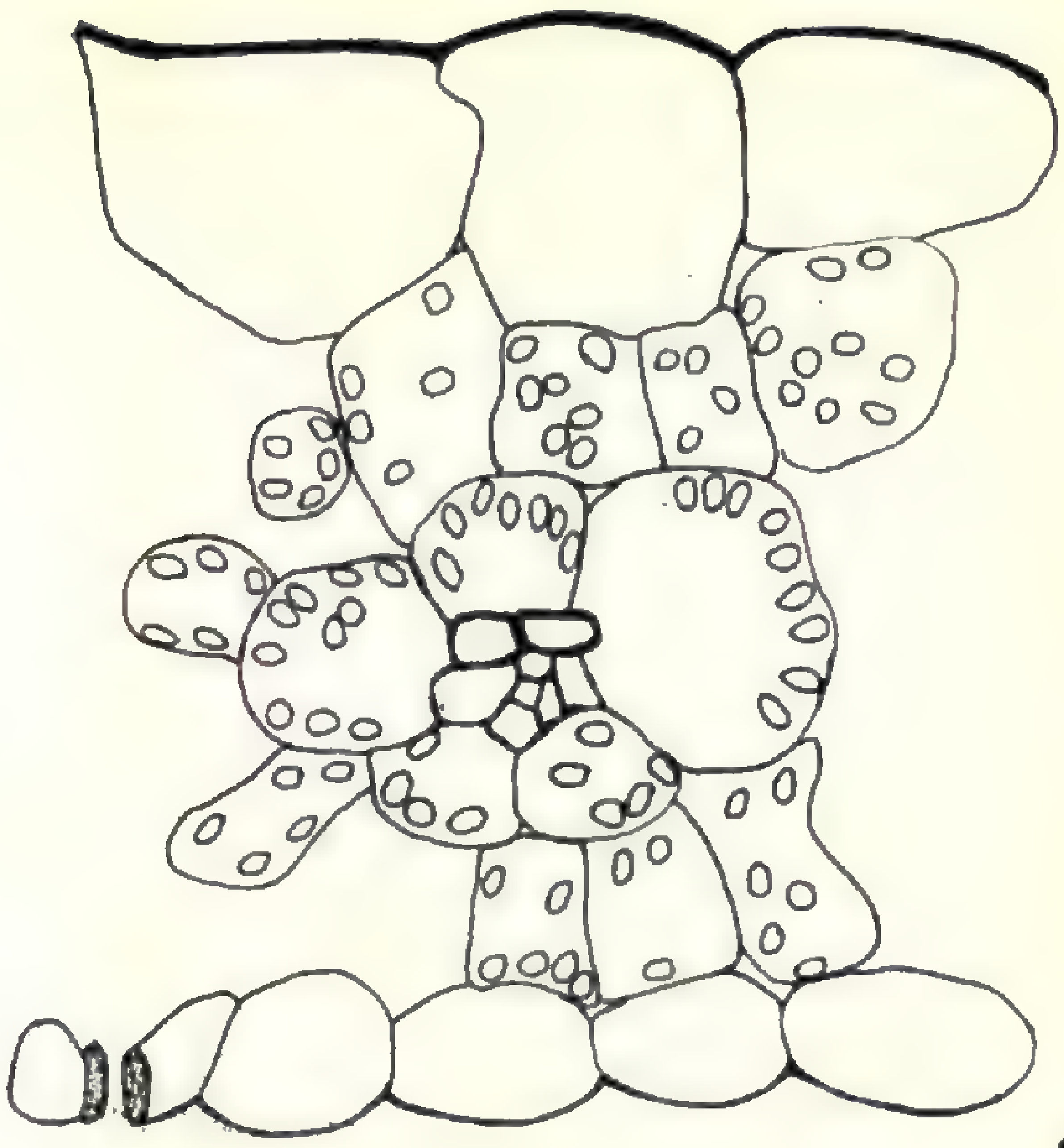

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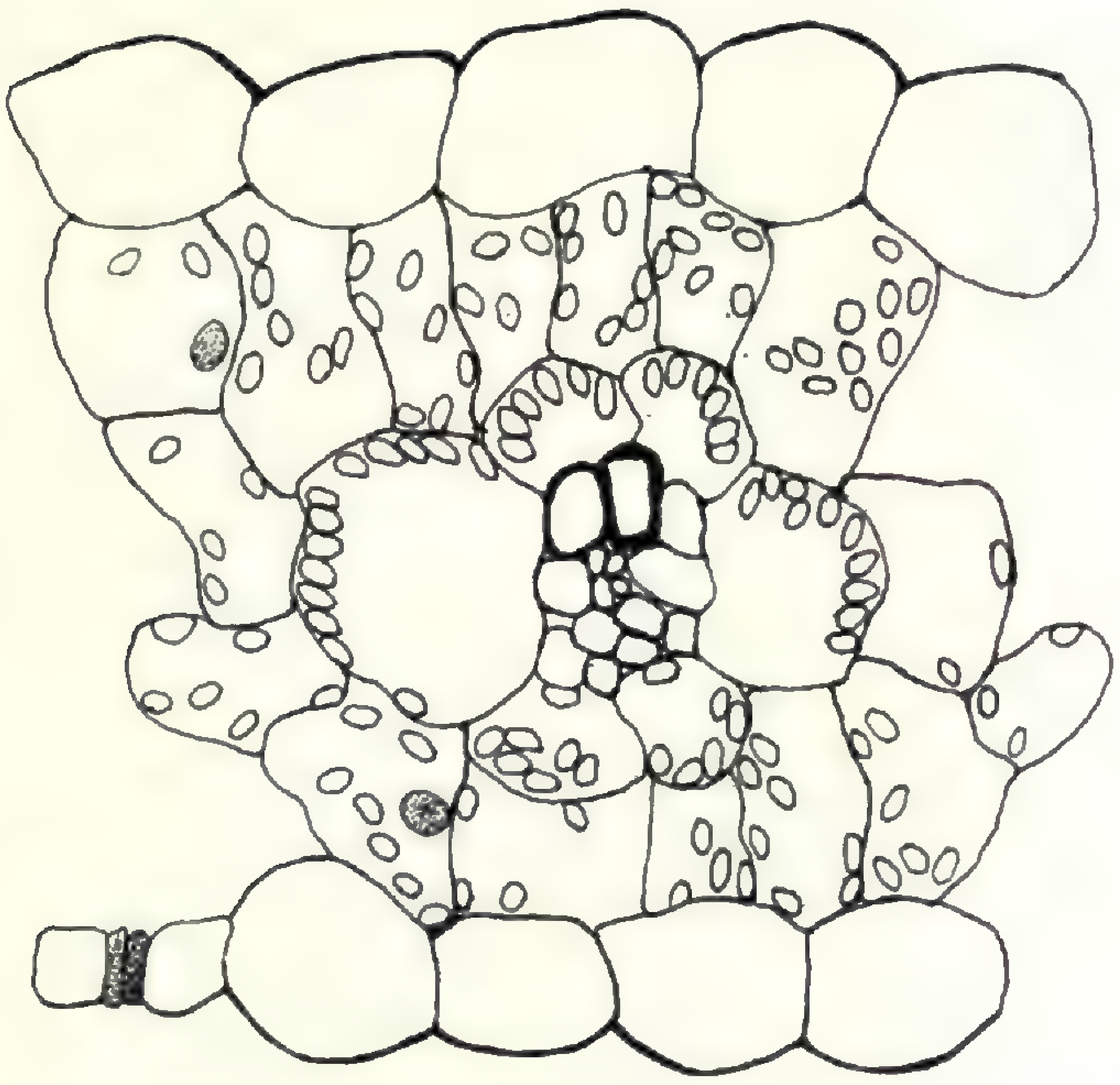

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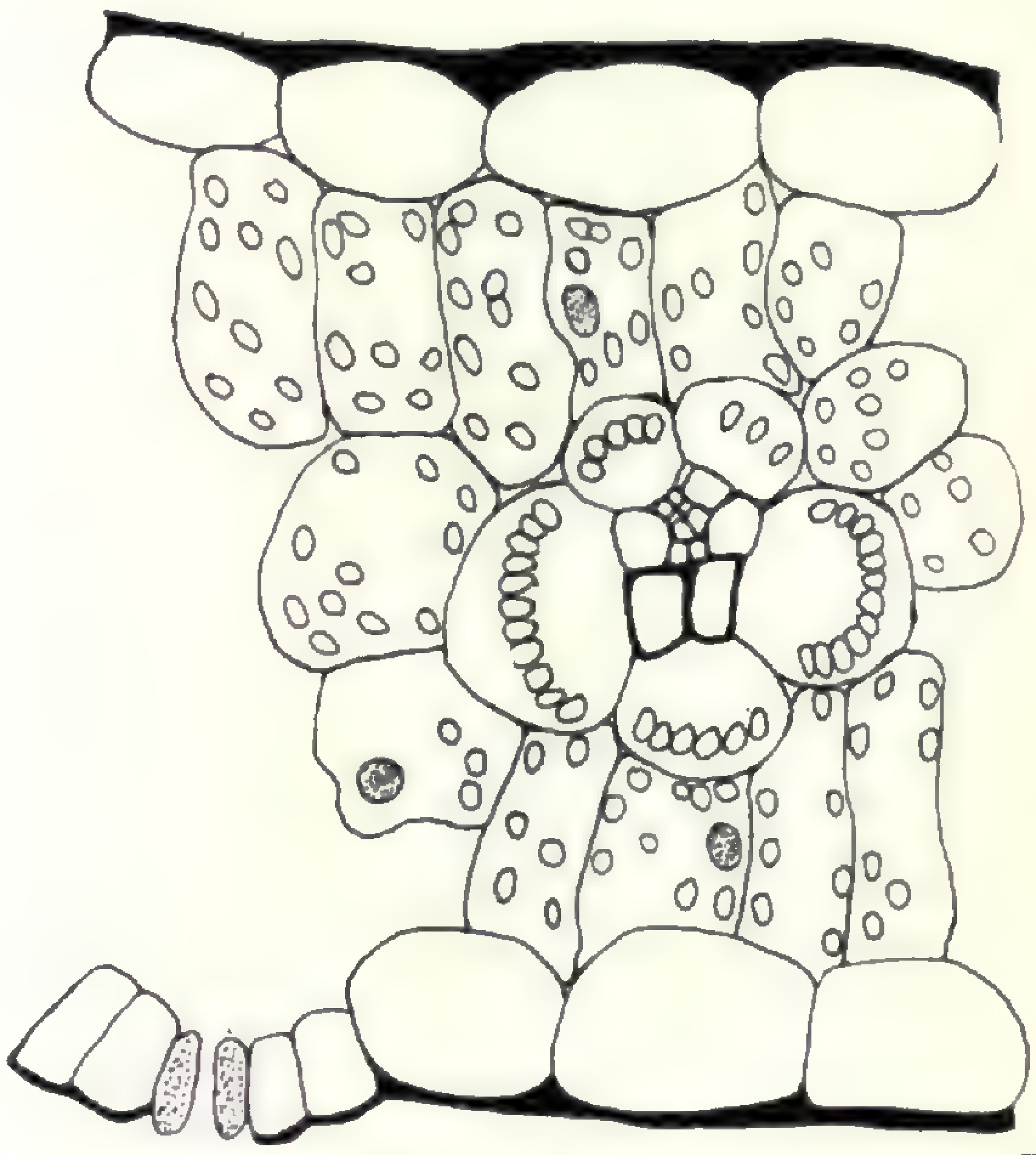

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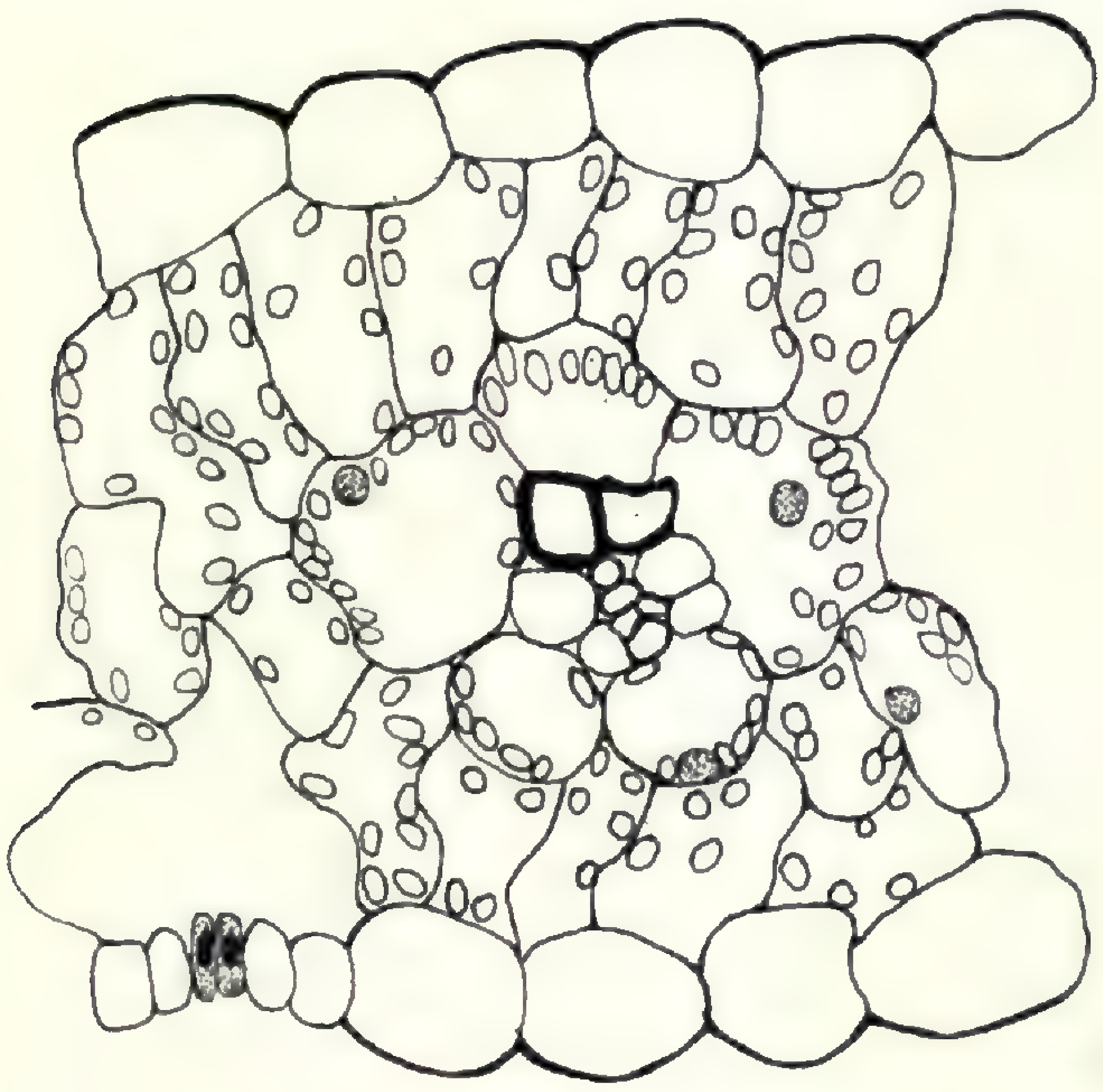

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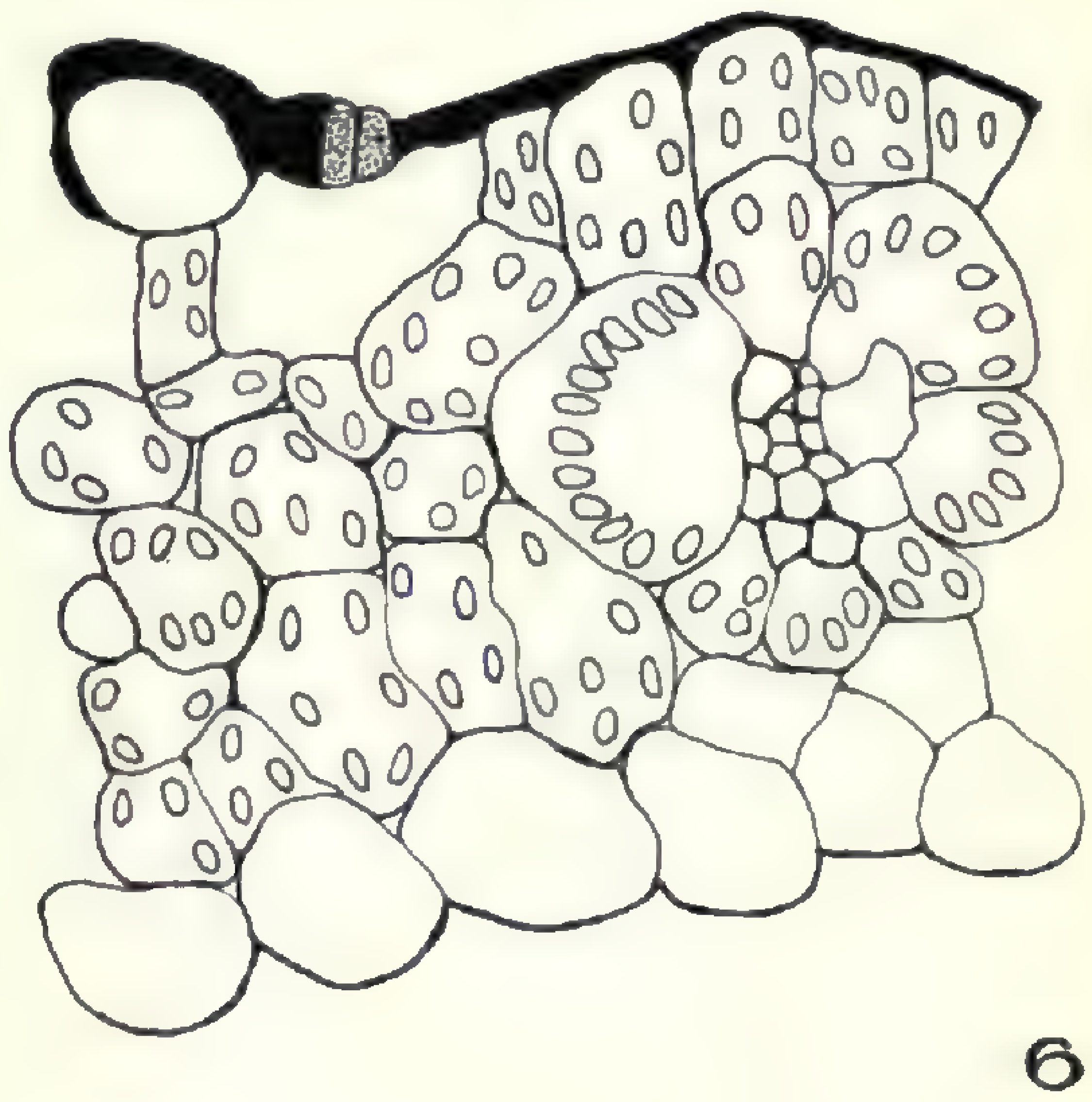


6

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Explanation of Plate

PLATE 33

Camera-lucida drawings of equal magnification, using 16-mm. objective and 10 × eyepiece. Corresponding bundles were used in all cases (sixth bundle from the epidermis).

Fig. 1. Cross-section of a fibrovascular bundle of *Zea Mays* from an unrayed stem.

Fig. 2. Cross-section of a fibrovascular bundle of *Zea Mays* from a stem rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

Fig. 3. Cross-section of a fibrovascular bundle of *Zea Mays* from a stem rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

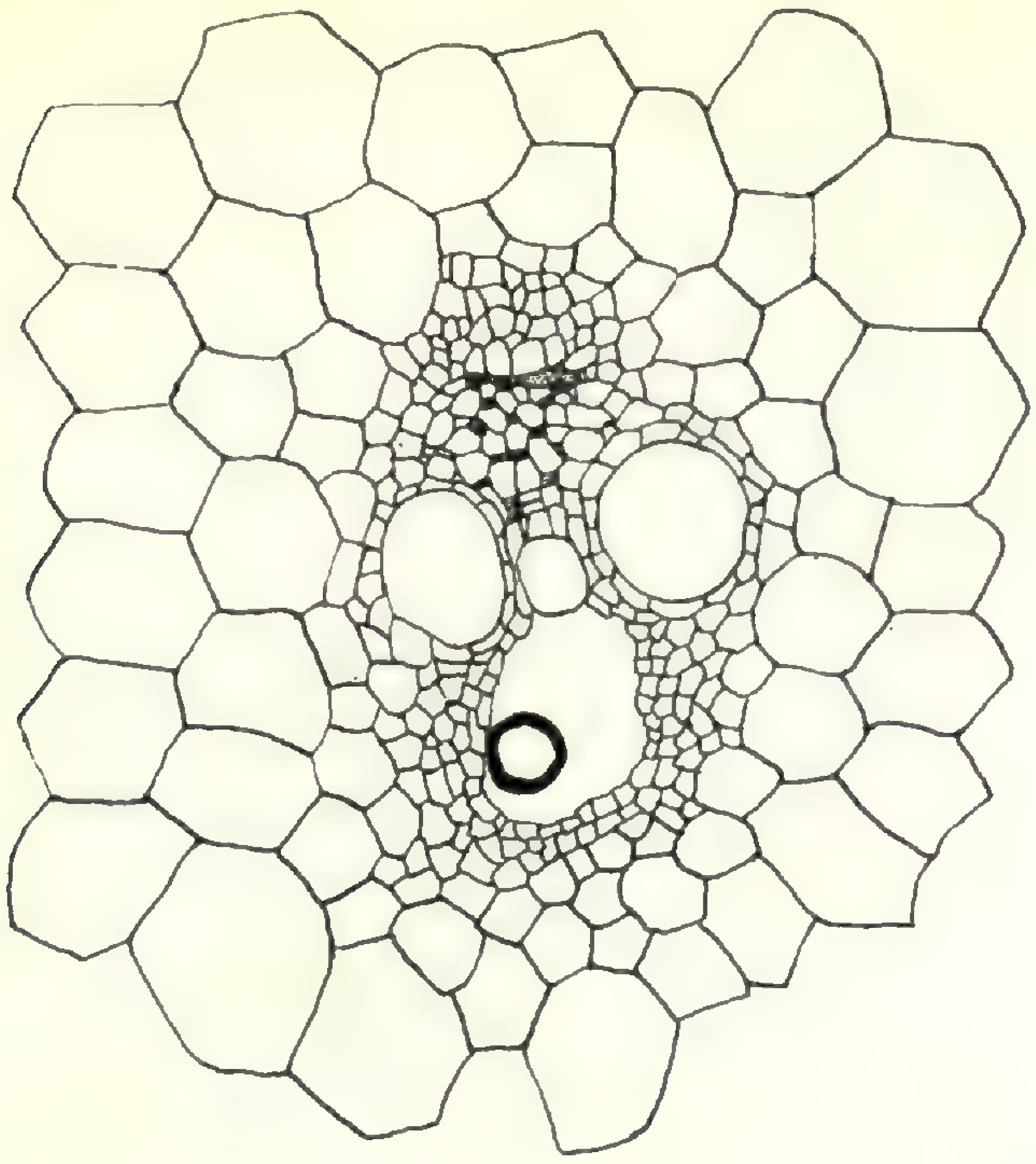
Fig. 4. Cross-section of a fibrovascular bundle of *Zea Mays* from a stem rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

Fig. 5. The amount of cortex present in a stem of *Zea Mays* rayed for seven weeks at 50 inches from the light, using a screen of quartz-lite glass.

Fig. 6. The amount of cortex present in a stem of *Zea Mays* rayed for seven weeks at 50 inches from the light, using a screen of vita glass.

Fig. 7. The amount of cortex present in a stem of *Zea Mays* rayed for seven weeks at 100 inches from the light, using a screen of vita glass.

Fig. 8. The amount of cortex present in an unrayed stem of *Zea Mays*.



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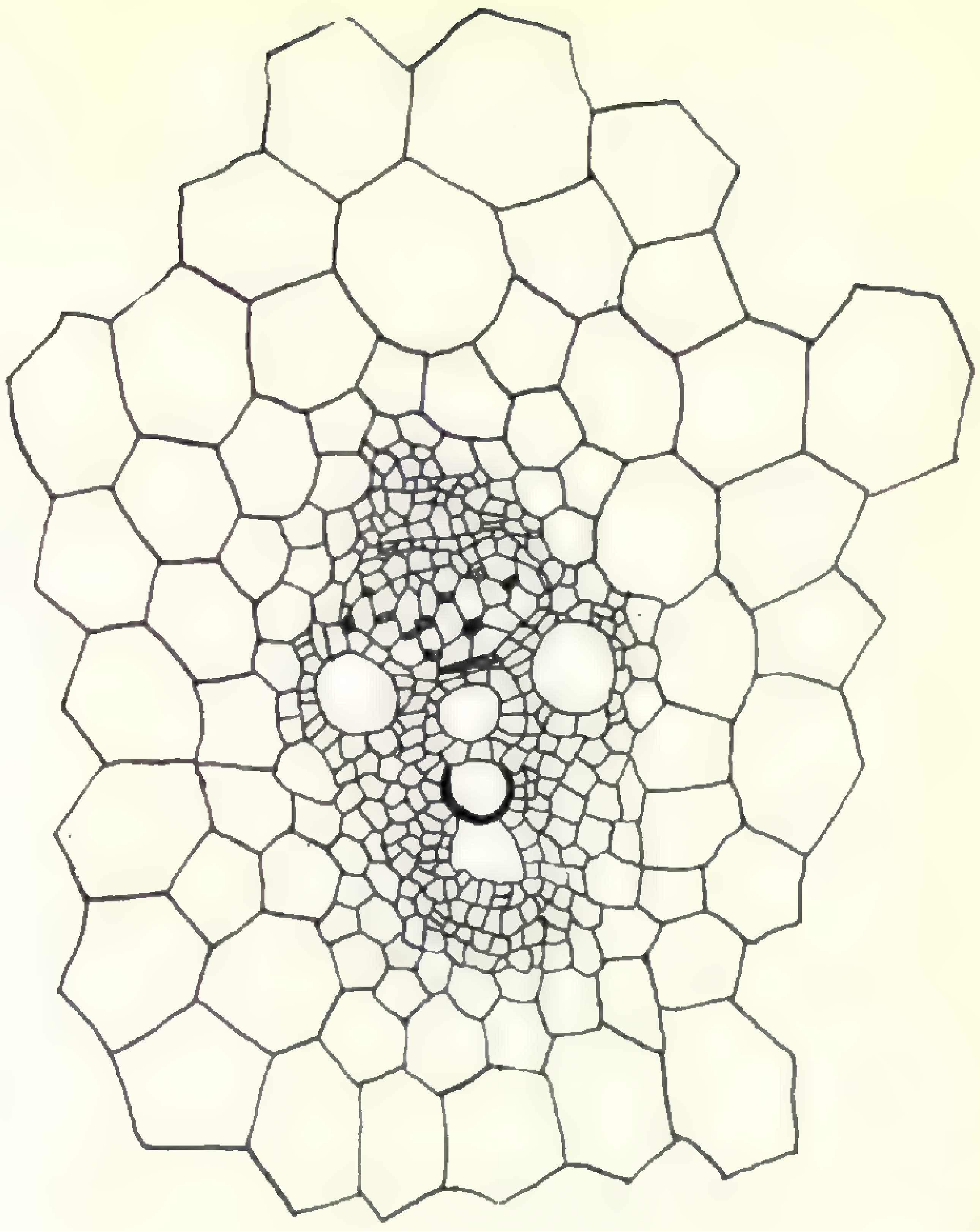

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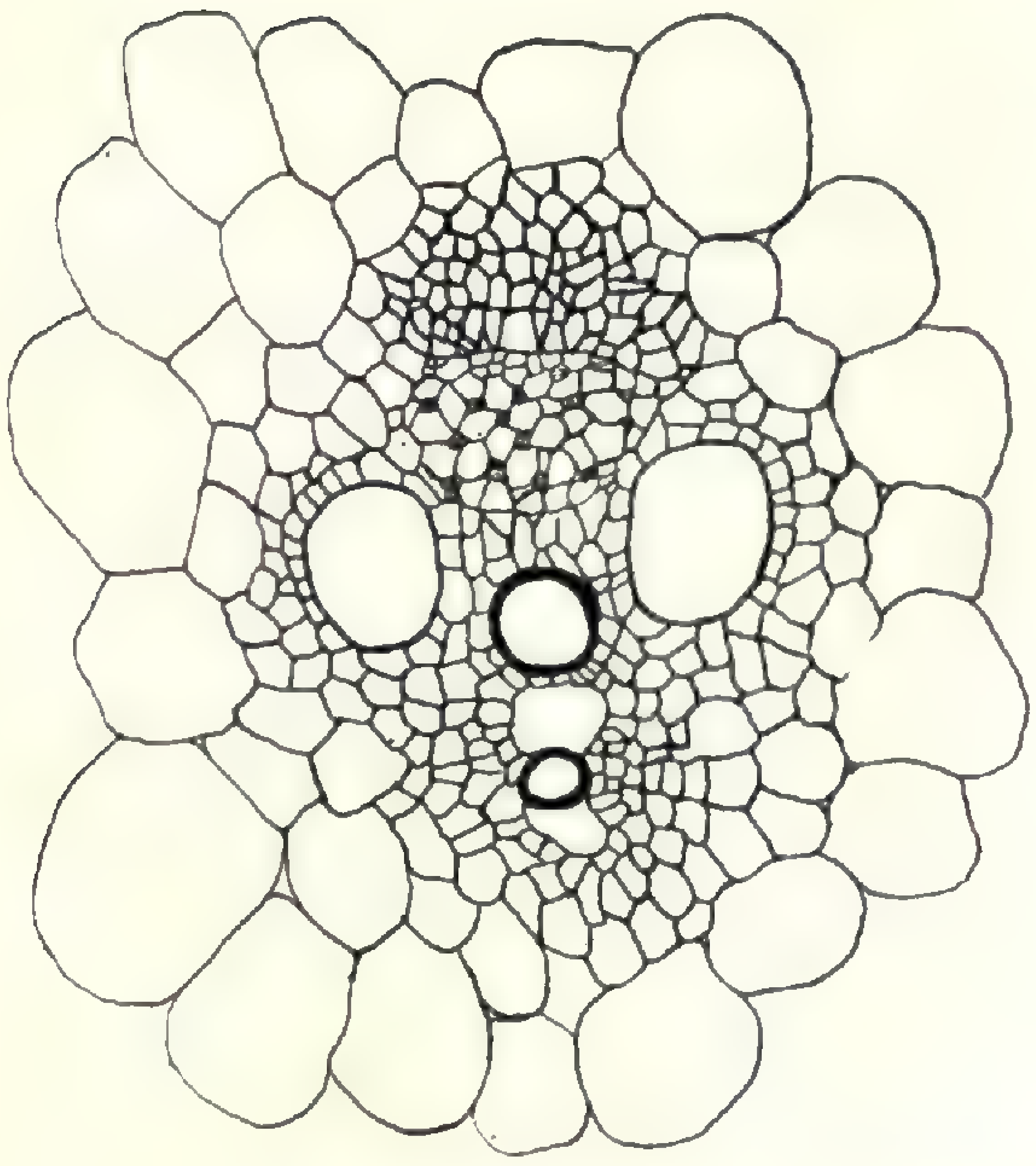

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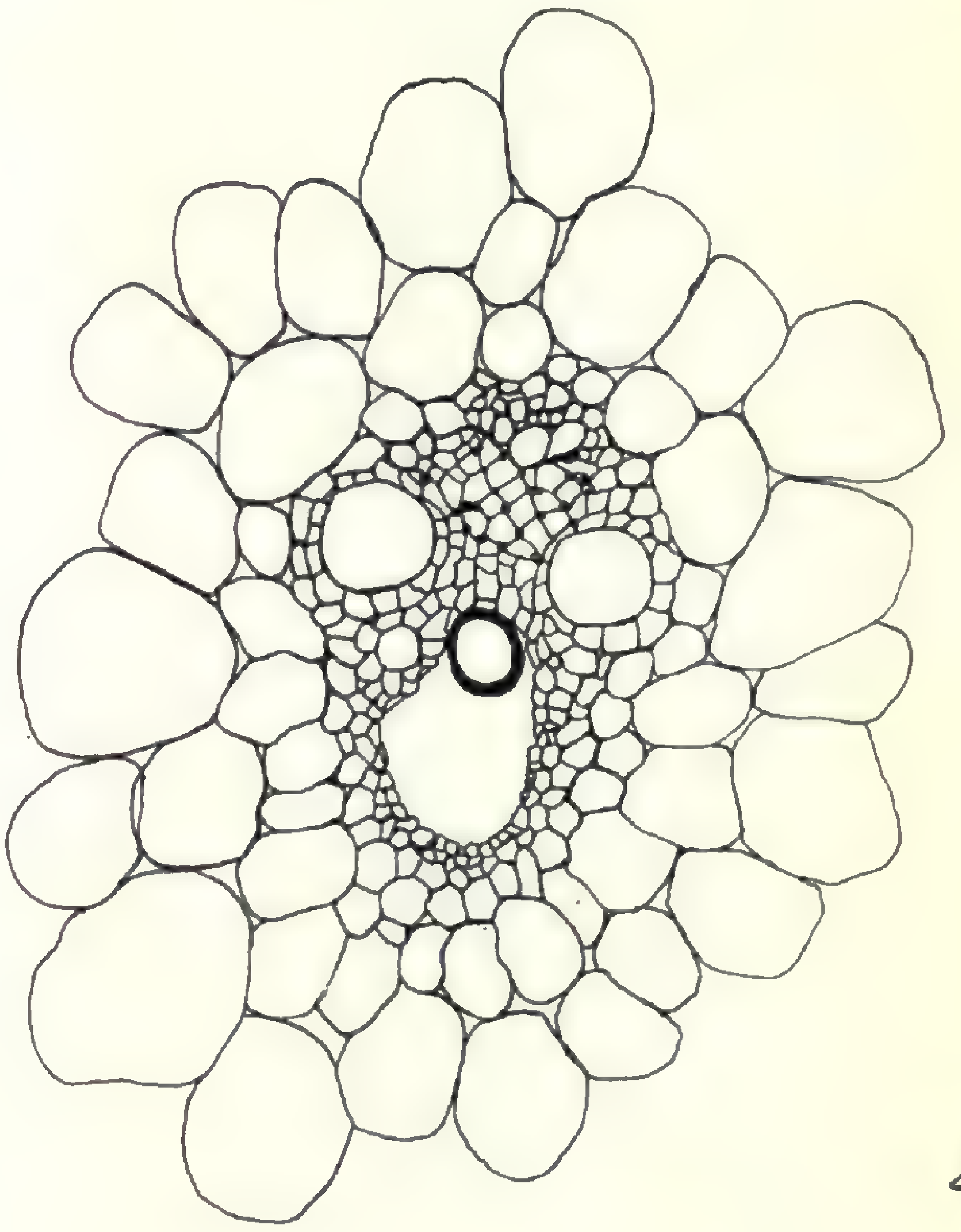

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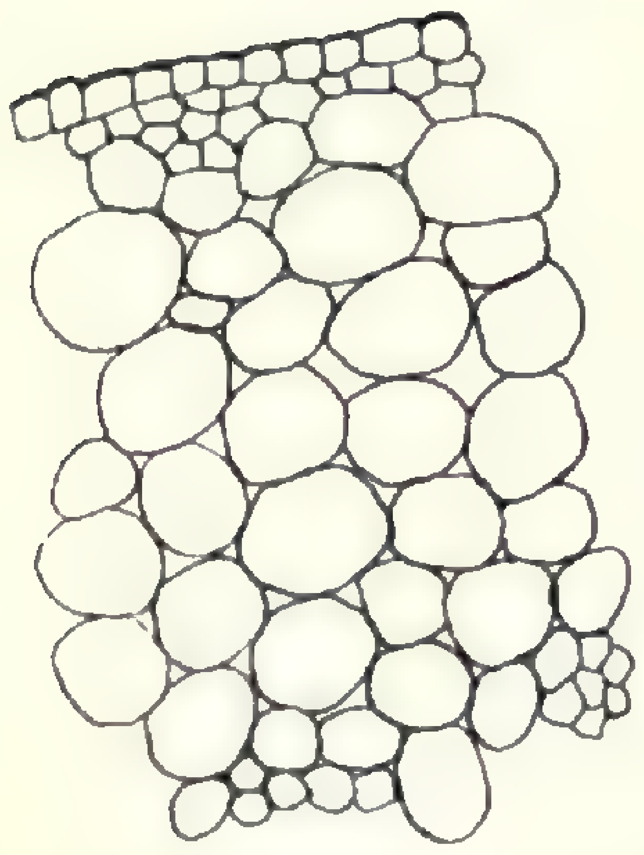

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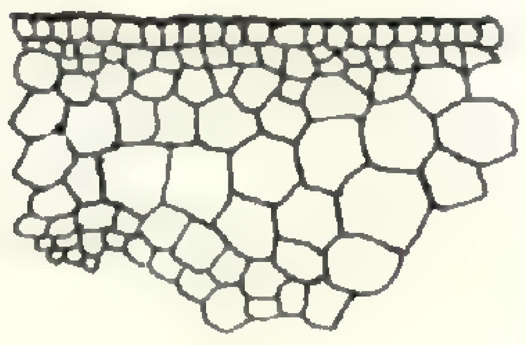

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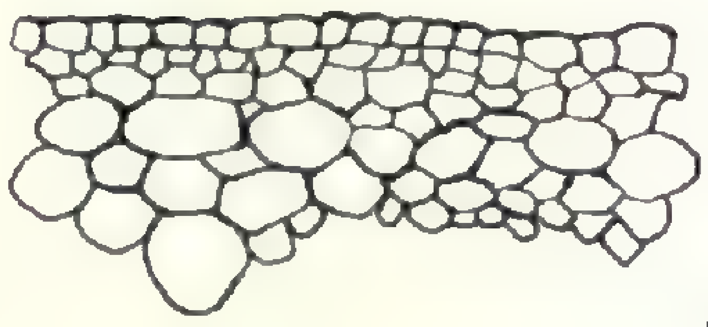

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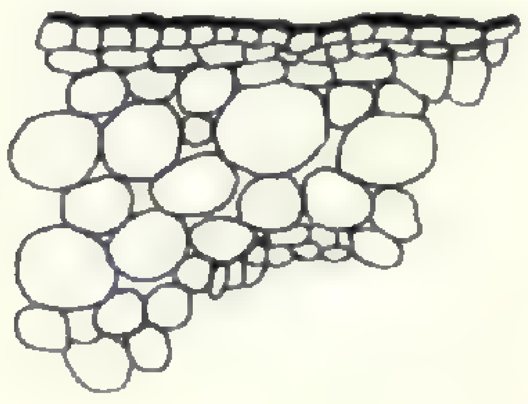

8

ELTINGE—EFFECT OF ULTRA-VIOLET RADIATION

Annals
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THE PROBLEM OF SPECIES IN THE NORTHERN BLUE FLAGS, IRIS VERSICOLOR L. AND IRIS VIRGINICA L.

EDGAR ANDERSON

Geneticist to the Missouri Botanical Garden
Assistant Professor of Botany in the Henry Shaw School of Botany of Washington University

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I. Introduction

The problem of species is a dual one. It asks two questions: What are species? How have they originated? In studying the nature of species we are first of all concerned with the extent to which the species of the orthodox taxonomists reflect actual divisions among plants and animals. Do such species, in the main, rest upon discrete natural groups of individuals or do they represent merely an artificial cataloguing device, ordering up, as best they may, the myriad forms occurring in nature.

It might be supposed that upon so fundamental a problem biologists would have come to some working agreement. Even the most casual survey of recent literature will show that this is far from being the case. While several of those who have committed themselves to print on the subject may use such phrases as "modern biologists recognize this to be the case," or, "all geneticists agree, etc., etc.," it is a noteworthy fact that no two of them are of the same shade of opinion. At one extreme are those who believe with Lotsy ('16) that, "The species is merely a

conception of the human mind and a very primitive anthropocentric conception in the bargain. * * * The species of the taxonomist is the comparative insignificant rest of large swarms of individuals which arose from the cross of two parents. * * * Species in the present taxonomic sense do not exist." On the other hand, we have such statements as Harper's ('23) "Linnean species do, by and large, constitute recognizable groups of more or less freely inter-breeding individuals. Only extremists deny the possibility of segregating and recognizing such units."

The disagreement as to species is just as extreme in regard to their size as in regard to their nature. If groups corresponding to our species do occur in nature, do they fit most readily into the species of the orthodox taxonomists (what we may call Linnean species for want of a better name) or would some other unit better express the relationships which we actually find among individuals? What are we to do with the vexed question of true-breeding sub-groups (variously termed micro-species, Jordanons, isoreagents) whose existence has been demonstrated for numerous Linnean species? Are we to retain them as significant sub-groups within the Linnean species, are we to treat them as of even greater importance, or are we to cast them out altogether?

It should be a relatively simple matter to answer these questions for any one species. A comprehensive survey of variation within the species over its entire range would show whether it were an independent unit or whether it merged into other forms; whether there were recognizable sub-groups within it; and what interrelationships obtained between the individuals which go to make up these sub-groups and the species itself.

However, such an intensive study should be able to contribute to other questions besides the nature of species. It should offer valuable evidence for the more popular question of their origin. During the last quarter of a century an attempt has been made to study evolution experimentally. In the course of these experiments two types of mutations have been observed in our laboratories and breeding plots. They have been thought to be the same sort of changes which, operating in the past, have brought about the evolution of our present-day forms. The first type of mutation has been shown to be due to changes which take

place at a particular point in the germ-plasm. Since only a single gene is affected, such changes have been called gene-mutations.

The second type of mutation has been shown to be due to re-alignments of the germinal material, to duplications of chromosomes or whole sets of chromosomes. The morphological results of these two types of mutation are quite dissimilar. An intensive and extensive survey of variation within a single species should therefore be able to demonstrate which of these two processes has been most active in causing progressive changes within that species. Such a study should, in other words, enable us to evaluate the evolutionary importance of gene-mutations and chromosomal re-alignments.

The present study is just such an intensive and extensive survey of two closely related species. It is an attempt to present a fairly complete picture of the variation within two natural groups of individuals over their entire range. It has as yet been almost purely morphological in scope. Though the morphological differences between individuals and groups of individuals undoubtedly rest upon basic physico-chemical ones, our knowledge of these physiological differences is as yet too incomplete, among the flowering plants, to possess much phylogenetical significance.

So far as is known, no such complete survey of variation within a species or group of species has ever before been made with plant material. It is an ambitious attempt for a single individual unless the problem be made as simple as possible. If we are to learn anything about the ultimate nature of species we must first of all reduce the problem to the simplest possible terms and study a few easily recognized, well-differentiated species. The group to be studied should therefore possess few sub-groups and intergrading forms. Unfortunately those species which have been selected for intensive study in the past have been chosen by reason of their very complexity.

The northern blue flags (*Iris versicolor* of the seventh edition of Gray's 'Manual') were accordingly chosen for the study, primarily, because they were a comparatively simple, stable, and well-marked group. They possessed certain other features which have materially reduced the labor involved in locating and study-

ing a large number of individuals. They are common, conspicuous, colonial, and perennial. Though the merits of these characters are practically self-evident, it may not be out of place to call attention to the colonial nature of *Iris versicolor* L. and its close relatives. Plants of these species are seldom found as isolated individuals but usually occur in colonies of a few to several hundred plants. Nor are these colonies merely the vegetative offspring of a single plant as is the case with so many colony-forming species. The individuals vary so strikingly in the size, shape, and color of their flowers, that at blooming time the limits of a single clone can readily be determined. These seldom exceed a few square feet, though exceptionally large clones do sometimes occur, as will be described below. It was the truly colonial nature of the blue flags which was particularly useful in the present study, making possible the examination of large numbers of plants in each locality with a minimum of effort.

An attempt was made to visit as much as possible of the range of the northern blue flags during their flowering season. Numerous colonies were studied in detail and measurements made on twenty to fifty individuals of the characters which had been selected for study. Representative plants were sent back from each of the colonies and established in an experimental plot at the Missouri Botanical Garden, where they were made the subject of genetical, morphological, and cytological studies.

In 1923 collections were made in central Michigan. In the spring of 1924 a trip was taken through northern Missouri, eastern Iowa, southern Wisconsin, central Michigan, western New York, and central New Hampshire. In 1925 collections were made in central Missouri, northwestern Arkansas, northern Ohio, including the Bass Islands, western and central New York, and southern Vermont. Fruiting material was collected that fall from central and northern New Hampshire and eastern Michigan. In the spring of 1926 a trip was taken through southern Illinois, southern Missouri, eastern Arkansas, western Tennessee, and central Kentucky. In June, collections were made in Missouri, Michigan, northern Vermont, Ottawa, Canada, and at Lake Timagami, in northern Ontario, Canada. In the early spring of 1927 another southern trip was taken, principally

to collect material from Mississippi and Alabama. In June of that year collections were made in Ohio, Maryland, Pennsylvania, New York, Ontario, northern Michigan, and Wisconsin. In 1928

Fig. 1. Localities at which *I. versicolor* and *I. virginica* have been studied.

North and South Carolina and eastern Tennessee were visited in early May. With the exception of the extreme north the territory has now been quite thoroughly covered as shown by the map in fig. 1.

Extensive collections of flowering material preserved in alcohol and of ripe seed capsules were made at several points by Mr. R. E. Woodson, Jr. and by the writer. The work on the fresh and preserved material has been supplemented by taxonomic studies in the herbarium of the Missouri Botanical Garden and at various other herbaria.

ACKNOWLEDGEMENTS

It is scarcely possible to carry on a study involving geographical distribution without enlisting the help of a very large number of people. For aid in assembling information and material for study it is a pleasure to acknowledge the cooperation of those whose names are listed below, and of several others who have been inadvertently overlooked:

Dr. J. R. McLeland, R. W. Shreve, A. N. Rood, R. S. Sturtevant, W. M. Boswell, Dr. A. C. Kinsey, Dr. P. C. Mangelsdorf, Prof. J. G. Jack, Dr. J. N. Couch, E. A. Mosley, Mr. Holtiwanger, Dr. O. E. Jennings, John MacDougal, A. F. Satterthwaite, M. E. Mains, Miss G. V. Butcher, Mrs. Jasper Blackburn, A. C. Anderson, Herbert Stoddard. Miss Katherine Perkins, Mrs. Will Spear, Miss Edith Mason, J. B. Stevenson, E. J. Layton, Henry Edmonds, J. E. Gilmour, J. Steyermarck, John H. Rush, Miss Martha Beardsley, Mrs. Dorothy M. Anderson, Phil Rau, Miss Mildred Mathias, Miss Katherine H. Litch.

Sincere appreciation is due the curators of the United States National Herbarium, the Gray Herbarium of Harvard University, the Dillenian Herbarium, the herbaria of the Field Museum, of the University of Wisconsin, of the Michigan State College, of the Philadelphia Academy of Natural Sciences, of the Linnean Society, and the British Museum, for the opportunity of studying material from these institutions. Thanks are also due Professor J. Paul Goode, of the University of Chicago, for permission to use his Homolosine Equal Area Projection Map (fig. 1.)

For much advice and helpful information in connection with the taxonomic aspects of the problem, the author is deeply indebted to his colleague, Dr. J. M. Greenman. For watchful care of the experimental garden during his absence he is pleased to thank Mr. P. A. Kohl. The study would have been less complete in many ways but for the assistance of Mr. R. E. Woodson, Jr. in

making the collections and tabulating the data. It is a pleasure to acknowledge his helpful companionship and material aid.

II. Taxonomy and Morphology

HISTORY OF THE SPECIES

It has been found that what commonly passes for *Iris versicolor* L. is made up of two species. One, inhabiting New England, New York, Pennsylvania, northern Ontario, and northern Michigan, has lanceolate petals much shorter than the sepals, a short ovary, and shiny D-shaped seeds. The other extends in the middle-western states from the Great Lakes to the Gulf of Mexico and up the Atlantic seaboard to southern Virginia. It has obovate-spatulate petals which are nearly as long as the sepals, a long ovary, and dull, round or D-shaped seeds. As will be brought out in Parts III and IV of this paper, the species are wholly distinct and crosses between them are partially sterile. Their distribution is shown in more detail in fig. 1.

It now becomes necessary to determine their relation to the species named by Linnaeus. In the first edition of the 'Species Plantarum' he named, as numbers 10 and 11, two similar American irises. To the first, which he named *Iris versicolor,* he referred numbers 187 and 188 of Dillenius and the *Iris latifolia Virginiana* etc. of Ehret. The second he named *Iris virginica,* basing it upon Gronovius' *Iris corollis imberbibus,* etc. The two species of *Iris* studied by the writer are very similar to each other and, like many other species of the genus, are difficult of recognition in ordinary herbarium specimens. Were it not for the fact that we have such ample material it might be difficult, if not impossible, to determine the relation between the names given by Linnaeus and these two common species of eastern North America.

Fortunately there are such good illustrations and such excellent herbarium specimens that there can be no doubt that the common blue flag of the East and North is identical with *Iris versicolor* of Linnaeus and that the species of the South and Middle West is identical with his *Iris virginica.*

For *Iris versicolor* I have studied figs. 187 and 188 of Dillenius, Tab. VI and VIII of Ehret (pl. 35), and a photograph (pl. 36, fig. 1) of Dillenius' specimen in his herbarium at Oxford. Ehret's

excellent figures leave no doubt about the identification. Particularly to be noticed are the short ovary, the lack of auricles on the dissected style, the broad-bladed sepal, and the lanceolate petals. Dillenius' figure and his specimen show very small petals; the herbarium specimen in addition has a short ovary.

In the case of *Iris virginica,* I have examined Clayton's No. 259 at the British Museum, and Linnaeus' own specimen of *Iris virginica* at the Linnaean Society. Both are in an excellent state of preservation and each shows heavy pubescence on the blade of the sepal.

Jacquin's plate of *Iris virginica* is an excellent figure of *Iris versicolor.* It shows a plant with small petals, sepals with no trace of a yellow eye, and long pedicels.

The plate (pl. 36, fig. 2) accompanying Radius' description of *Iris carolina* shows it to be identical with *Iris virginica.* The sepal and petal are both waved, a character often assumed by *Iris virginica,* never by *Iris versicolor.* The petals are nearly as long as the sepals, and according to the description the plants have few flowers. Furthermore, the species is distinguished from *Iris virginica* of Linnaeus, according to Jacquin, which as we have seen, is *Iris versicolor* of Linnaeus.

Plants from the same general region were described as *Iris caroliniana* by Watson in 1898. In his description he speaks of "the elliptical blade lilac, veined with purple and with a yellow spot reaching to the center." The petals are described as oblong-spatulate. The type specimen, in the Gray Herbarium, shows the typical roundish seeds with a spongy surface, which characterize *Iris virginica.* Material from practically the same locality was studied in the spring of 1928 by the writer. When large numbers of plants were examined there was found to be no consistent difference of any sort between the irises of the Carolina Coastal Plain and those of the Mississippi Valley. There is therefore no ground for maintaining *Iris Shrevei* of Small. He distinguishes it from *Iris versicolor* but makes no mention of its relationship to *Iris carolina* (*Iris virginica* L.), with which it is identical. The illustration accompanying his description is evidently made from a badly stunted plant. Specimens collected from the same locality visited by Small are much larger than those

in his illustration. The locality was visited when the plants were in full bloom and nearly all bore the bright yellow-pubescent spot on their sepals which shows in his illustration of *Iris carolina* but is lacking from his illustration of *Iris Shrevei.* Furthermore, plants transplanted from that locality to the experimental garden have borne as many round as D-shaped seeds, though his illustration shows only a D-shaped seed.

COMPARATIVE MORPHOLOGY

Distinguishing differences in italics. See also pls. 37–39, 41–43.

	IRIS VIRGINICA L.	IRIS VERSICOLOR L.
ROOTSTALK	A creeping rhizome *2.0–4.0* cm. in diameter. Stele, in fresh specimens, yellowish white to dirty yellow. Cortex pale pinkish white.	A creeping rhizome *1.0–2.5* cm. in diameter. Stele, in fresh specimens, yellowish white to dirty yellow. Cortex pale pinkish white.
ROOTS	Wrinkled, *2–4 mm.* in diam., white.	Wrinkled, *1–3 mm.* in diam., white.
LEAVES	Narrowly ensiform, *1–5 cm.* broad, gray-green, often flushed with purple below.	Narrowly ensiform, *0.5–3.0 cm.* broad, gray-green, often flushed with purple below.
STEM	*Sparingly branched* above, green or greenish purple.	*Freely branched* above, green or greenish purple.
SPATHE VALVES	*4–12* cm. long, *occasionally* becoming foliaceous.	*3–4.5 cm.* long, *never* becoming foliaceous.
PEDICELS	*2.5–8.0 cm.* long in the flower, *rarely equalling* the longest spathe valve.	*1.0–8.0 cm.* long in the flower, *often equalling or surpassing* the longest spathe valve.
OVARY	*1.8–3.8 cm.* long in the flower; ovary wall relatively *thick; ovules nearly filling locules at anthesis.*	*0.8–2.0 cm.* long in the flower; ovary wall relatively *thin; ovules filling scarcely half the locules at anthesis.*
TUBE	Wall of tube *thick, conspicuously glandular, closely appressed to style base within.*	Wall of tube *thin, not conspicuously glandular, style base distinctly separate from tube.*

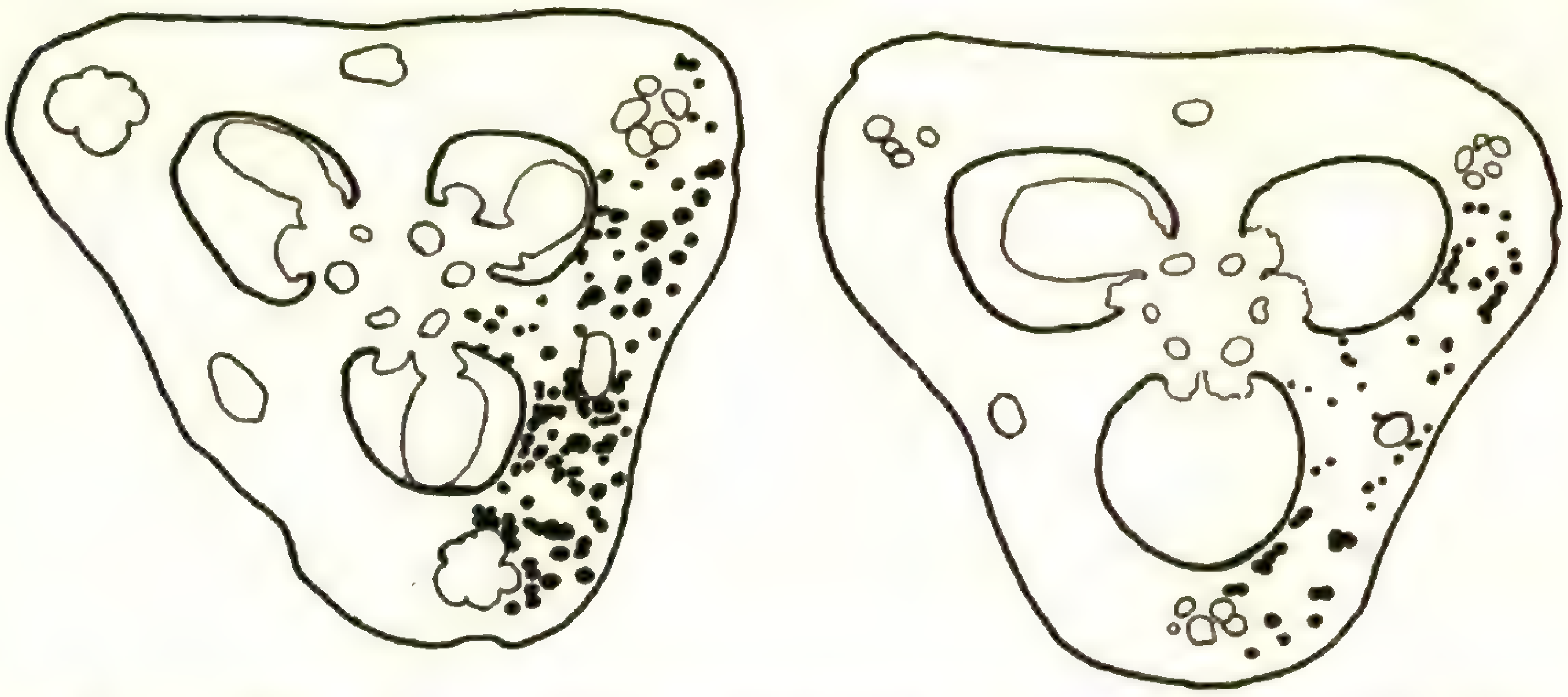


Fig. 2. Camera-lucida drawing of cross-sections of ovaries of *I. versicolor* (right) and *I. virginica* (left), resin ducts in black, vascular bundles outlined; × 10.

SEPALS	
4.0–8.4 cm. long, *1.6–4.0 cm.* broad; blade of sepal *oblong-ovate* to *ovate*, usually some shade of *bright blue*, although white and lavender specimens have been found.	*4.0–7.2 cm.* long, *1.8–4.0 cm.* broad; blade of sepal *ovate* to *reniform-ovate*, usually some shade of *purplish-blue*, although white and lavender specimens have been found.
Blade bearing a bright yellow conspicuously pubescent spot at the base.	*Blade often without a conspicuous spot at the base; when present, greenish or greenish yellow.*
Hairs of the pubescence *conspicuous* and *macroscopic, longer* than the thickness of the sepal.	Hairs of the pubescence *inconspicuous* and *microscopic, shorter* than the thickness of the sepal.
PETALS	
Oblong-lanceolate to *oblong-spatulate*, *3.0–7.0 cm.* long, *1.0–3.0 cm.* broad, *often* (in about 50 per cent of the cases) notched at the apex, of the same general color as the sepals, *delicate in texture, easily bruised, wilting readily.*	*Lanceolate* to oblong-lanceolate, *2.2–5.4 cm.* long, *0.5–2.2 cm.* broad, *very rarely* notched at the apex, of the same general color as the sepals; *firm in texture, not readily wilting.*
STYLE	
Style branches *inwardly auriculate* at their convergences.	Style branches *not auriculate* at their convergences, *or at most but weakly so.*
STYLE CRESTS	
Reflexed, variously toothed, *0.7–2.0 cm.* in height.	Reflexed, variously toothed, *0.7–1.5 cm.* in height.
Stigma a triangular tongue.	Stigma a triangular tongue.
STAMENS	
Anthers *0.9–2.1* cm. long.	Anthers *0.7–1.6* cm. long.
Pollen-grains oblong-ovate in outline.	Pollen-grains oblong-ovate in outline.

CAPSULE	
Capsular lining *irregularly* minute-striate; inner surface *mainly dull.*	Capsular lining *regularly* minute-striate, giving the inner surface a *uniformly shiny* appearance.
SEEDS	
Round to D-shaped in outline. Seed-coat *corky* and *dull*, the surface appearing *irregular, with occasional broad depressions* under a hand-lens.	*Always D-shaped* in outline. Seed-coat relatively *thin, hard,* and *shiny*, the surface appearing *regularly pitted*, the *pits in definite rows* under a hand-lens,

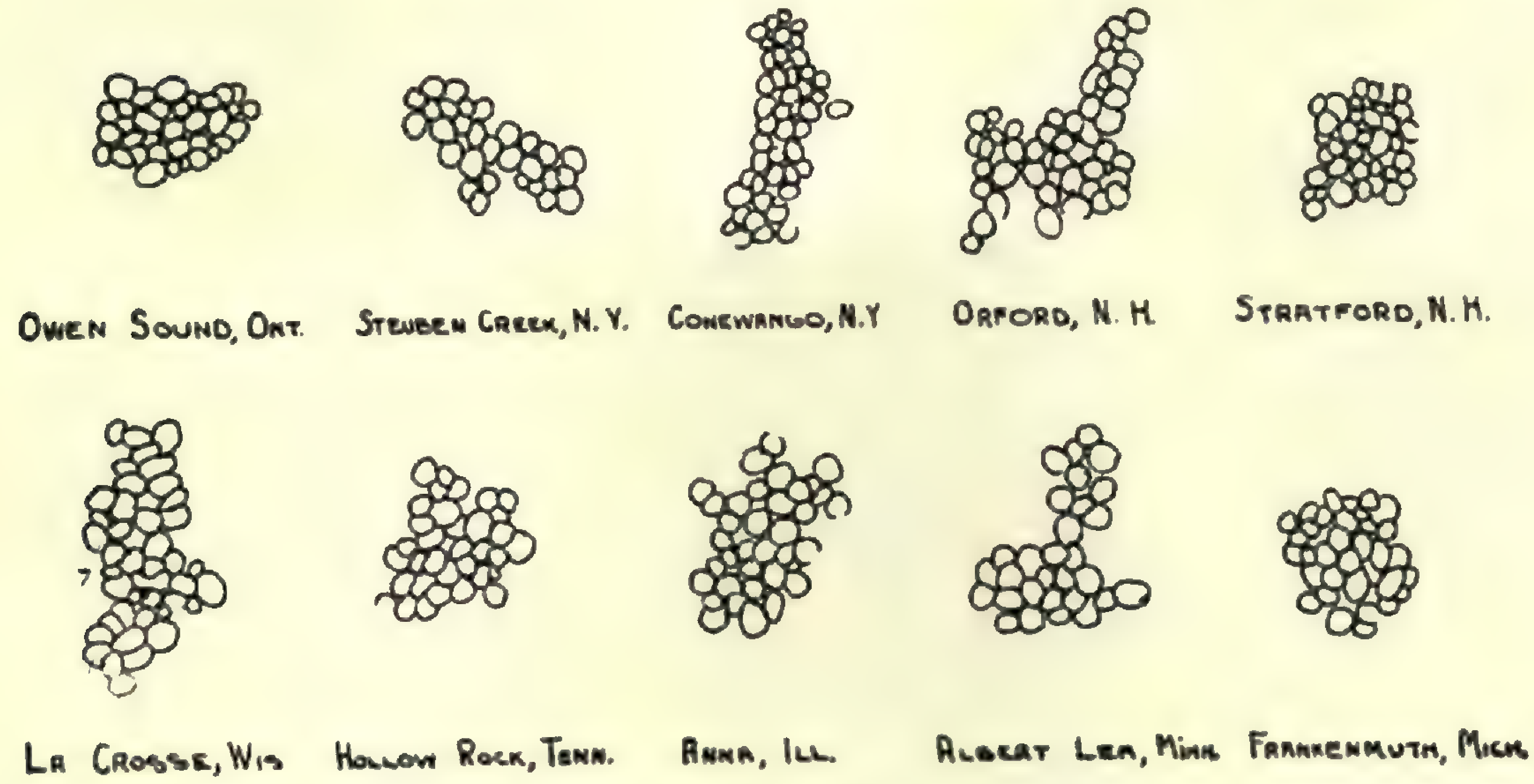


Fig. 3. Camera-lucida drawings of cells in outer seed-coat: upper row, *Iris versicolor*, lower row, *I. virginica;* × 20.

GEOGRAPHICAL DISTRIBUTION

It is planned to give a detailed discussion of the distribution of the two species in a later section. Until then certain outstanding points may be briefly summarized.

Iris versicolor is generally a northern and eastern species, *Iris virginica* a southern and central-western one. As shown by the map in fig. 1, *Iris versicolor* occurs in New England, New York, Pennsylvania, northern Michigan, Wisconsin, and Minnesota, and eastern Canada, *Iris virginica* extends from the Gulf states to central Michigan and Wisconsin and west to the eastern edge of Nebraska and Kansas. On the Atlantic coast it is common in the Carolina Coastal plain, though it is rare in the mountains and was not seen in the Piedmont.

At their zone of contact in Michigan, Wisconsin, and Minnesota, the range of *Iris versicolor* coincides very nearly with the northern

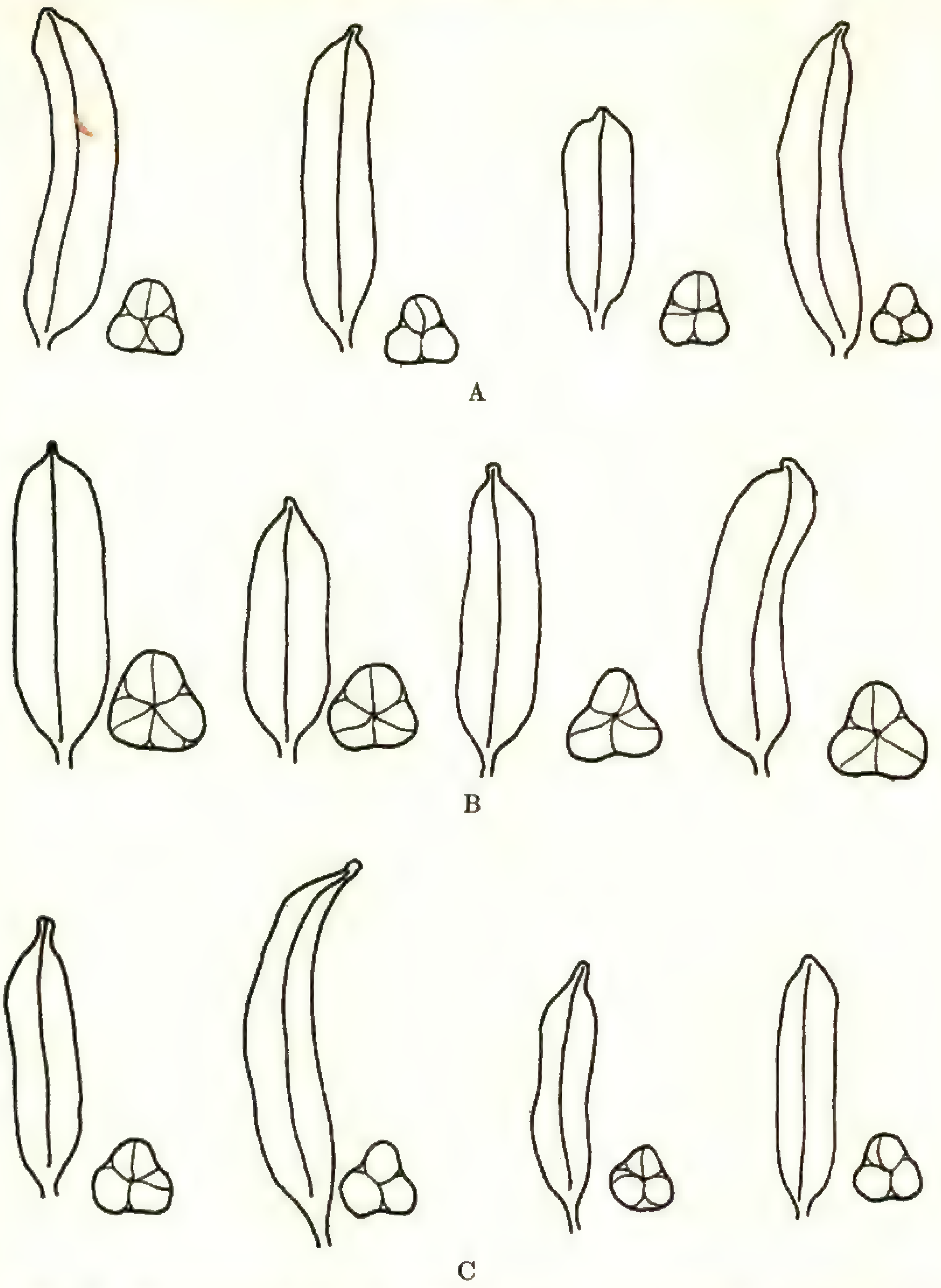


Fig. 4. Camera-lucida drawings of seed capsules showing outline and cross-section with seeds, × ⅓: *A*, *I. virginica*, from La Crosse, Wis.; *B*, *I. versicolor*, from Conewango, N. Y.; *C*, *I. virginica*, from Bonnieville, Ky.

coniferous forest, that of *Iris virginica* with the southern hardwoods.

Both species, while distinctly moisture-loving, belong to the border zone between marsh and dry land. They are not able to compete successfully if the situation is wet enough for *Typha* or dry enough for grasses. In those regions which have been completely drained and brought under cultivation they have very nearly disappeared. None were found in the drained areas of southeastern Missouri, though the species was formerly common there. Several local naturalists have reported that *Iris virginica* was much commoner in Tennessee and North Carolina before the lowlands in these states were brought under cultivation. In those sections of the country, on the other hand, where such areas have been left as pasture lands, both species have increased. Livestock eat the grass in preference to the Iris, and the iris colonies spread out vigorously, often covering several acres.

The seeds of both species float easily, and seedlings can often be observed coming up on wet sandy beaches of the Great Lakes. It would not be surprising to find *Iris virginica* establishing itself locally along the St. Lawrence River system. Two such colonies have actually been found: one on a deserted lake beach at Saint Ignace, and one on the shores of the Niagara River a few miles above the Falls on the American side.

ABBREVIATIONS

The abbreviations used to indicate the herbaria in which the specimens occur are as follows:

ASP = Academy of Natural Sciences of Philadelphia.
BM = British Museum.
MBG = Missouri Botanical Garden.
US = United States National Herbarium.

TAXONOMY

Iris versicolor L. Sp. Pl. ed. 1, 39. 1753; Curtis, Bot. Mag. **1**: *pl. 21.* 1790; Redouté, Liliacées **6**: *pl. 339.* 1812; Edwards, Bot. Gard. **2**: *pl. 30, fig. 2.* 1812; Baker in Gard. Chron. N. S. **6**: 614–615. 1876; Meehan, Native Flowers & Ferns **1**: *pl. 36.* 1878; Millspaugh, Med. Plants **2**: *pl. 173.* 1892; Britton & Brown, Ill. Flora, ed. 1, **1**: 448, *pl. 1069.* 1896, in part; Small, Fl. Southeast. U. S. 306. 1903, and ed. 2,305. 1913, in part;

Gray's Manual, ed. 7, 299. 1908, in part; Britton & Brown, Ill. Flora, ed. 2, **1**: 537, *pl. 1328*. 1913, in part; Dykes, Genus Iris, 79–81. 1913, in part; Small, Addisonia **9**: 55–56, *pl. 316*. 1924.

Pls. 38, 40, 41 (left fig.); 42 fig. 2; 43 figs. 6–10.

[*Iris americana versicolor stylo non crenato* Dillenius, Hort. Eltham. t. 155, *pl. 187*. 1732.]

[*Iris americana versicolor stylo crenato* Dillenius, Hort. Eltham. t. 155, *pl. 188*. 1732.]

[*Iris latifolia Virginiana* . . . . .Ehret, Plantae Depictae *pl. 6 & 8*. 1748.]

Iris virginica L. acc. to Jacquin, Icones Plant. Rariorum **2**: *pl. 223*. 1786–1793.

Iris virginica L. Sp. Pl. ed. 1, 39. 1753; Michx. Fl. Bor. Amer. 22. 1803; Sims in Curtis' Bot. Mag. **19**: *pl. 703*. 1804; Baker in Gard. Chron. N. S. **6**: 615. 1876.

Pls. 34, 37, 39, 41 (right fig.); 42 figs. 1, 3, 4; 43 figs. 1–5; 44.

[*Iris corollis imberbibus*. . . . . .Gronovius, Flora Virginica, 11. 1739.]

Iris carolina Radius, Naturforsch. Ges. Leipzig Schrift. **1**: 158, *pl. 3*. 1822; Small, Addisonia **9**: 49–50, *pl. 313*. 1924.

Iris versicolor L. in part; Britton & Brown, Ill. Flora, ed. 1, **1**: 448, *pl. 1069*. 1896; Small, Fl. Southeast. U. S. 306. 1903, and ed. 2, 305. 1913; Gray's Manual, ed 7, 299. 1908; Britton & Brown, Ill. Flora, ed. 2, **1**: 537, *pl. 1328*. 1913; Dykes, Genus Iris, 79–81. 1913.

Iris caroliniana Wats. in Gray's Manual, ed. 6, 514. 1890; Baker, Handbook Irid. 12. 1892; Sargent, Gard. & Forest **6**: 334–335. 1893; Britton & Brown, Ill. Flora, ed. 1, **1**: 449, *pl. 1071*. 1896; Wats. in Proc. Am. Acad. **25**: 134. 1898; Small, Fl. Southeast. U. S. ed. 1, 306. 1903, and ed. 2, 305. 1913; Gray's Manual, ed. 7, 300. 1908; Stapf in Curtis' Bot. Mag. IV, **8**: 94, *pl. 8465*. 1912.

Iris versicolor L. var. *virgimea* L., ex. Baker (err. typ.), Handbook Irid. 12. 1892.

Iris georgiana Britton in Britton & Brown, Ill. Flora, ed. 2, **1**: 537, *pl. 1330*. 1913.

Iris Shrevei Small, Addisonia **12**: 13-14, *pl. 391*. 1927.

IRIS VERSICOLOR L.

Specimens examined:

CANADA:

NOVA SCOTIA: Canso, July 24, 1901, *Ward* (US); Sable Is., Aug. 16, 1913, *St. John 1184* (US).

NEW BRUNSWICK: Campobello Is., July 8, 1880, *Smith* (US).

ONTARIO: Lincoln Co., June 10, 1897, *McCalla* (US); Paris, vicinity, July 4, 1926, *Mathias 636* (MBG).

UNITED STATES:

MAINE: St. John River, July 22, 1917, *St. John & Nichols 2230* (US); Westbrook, June 8, 1906, *Ricker 50* (US); Fort Kent, river flats, July 10, 1908, *Mackenzie 3422* (MBG); Seal Harbor, swamp, June 28, 1887, *Redfield 7117* (MBG); St. Francis, gravelly shore of St. John River, Aug. 5, 1893, *Fernald 147* (MBG).

NEW HAMPSHIRE: Peterborough, Aug. 20, 1913, *Batchelder* (ASP); Shelburne, June 17, 1915, *Deane* (US); Shelburne, Oct. 28, 1915, *Deane* (US); Connecticut Lakes, Oct. 20, 1895, *Stevens* (US).

VERMONT: Brandon, swale, June 6, 1921, *Dutton* (MBG); So. Burlington, July 8, 1914, Knowlton (ASP).

MASSACHUSETTS: Dedham, June 13, 1897, *Greenman 2333* (MBG); Brookline, June 26, 1896, *Greenman 2321* (MBG); Granville, meadow brook, June 20, 1914, *Seymour 174* (MBG); So. Framingham, May 31, 1890, *Sturtevant* (MBG); Cambridge, May 29, 1901, *Floyd* (MBG); Nantucket, pond margin, July, 1923, *Mason* (MBG); Ashland, wet grounds, *Morong* (MBG); Nonquit, June 5, 1888, *Sturtevant* (MBG); Woods Hole, July 26, 1911, *Pennell 3164* (ASP); Wilbraham, June 12, 1876, *Pillsbury* (ASP); Boston, 1816, *Boott* (US); Marthas Vineyard, June 29, 1916, *Seymour 6158* (US); Nantucket, June 2, 1900, *Day 64* (US); Marthas Vineyard, Aug. 1888, *Harrison* (US).

CONNECTICUT: Middletown, May, 1836, *Bigelow* (MBG); exact locality and date lacking, *Wright* (MBG); Stratford, June 7, 1893, *Eames* (US).

NEW YORK: Otis Summit, July 27, 1903, *Williamson* (ASP); St. Regis Falls, June 28, 1903, *Hudson 31* (US); Ithaca, June 23, 1885, *Coville* (US); Van Courtlandt, June, 1893, *Pollard* (US); N. Harpersfield, June 21, 1906, *Topping* (US); Elizabethtown, swamps,

July 2, 1875, *Redfield 7911* (MBG); Ithaca, June 4, 1877, *Trelease* (MBG); east of Cherry Valley, July 2, 1926, *Mathias 652* (MBG); banks of Lake George, Aug. 24, 1856, *Engelmann* (MBG); locality lacking, 1840, *Short* (MBG); Bedminster, meadows, date lacking, *Perry* (MBG).

New Jersey: Vineland, Sept. 12, 1923, *Bassett & Long* (ASP); Camden, May 22, 1922, *Bassett* (ASP); Quaker Bridge, Sept. 11, 1923, *Dreisbach 1834* (ASP); Folsom, June 10, 1911, *Long 5940* (ASP); Cor's, Ocean Co., Oct. 11, 1910, *Long 5582* (ASP); Cold Spring, Cape May Co., June 1, 1911, *Brown* (ASP); Atlantic City, margin of meadows, June 3, 1875, *Redfield 7910* (MBG).

Pennsylvania: Lester, Delaware Co., May 28, 1912, *Findlay* (ASP); Chester Co., June 4, 1905, *Weston 164* (US); Harrisburg, Aug. 13, 1888, *Small* (US).

Maryland: Spesutic Is., May 25, 1879, *Smith* (US); Chestertown, Aug. 18, 1900, *Vanata* (ASP).

District of Columbia: Washington, May and June, 1878, *Ward* (US).

Michigan: Cheboygan Co., sedge pool, July 17, 1917, *Gates & Gates 10597* (MBG); Douglas Lake, Cheboygan Co., July 17, 1916, *Ehlers* (MBG); Burt Lake, Cheboygan Co., July 4, 1917, *Gates & Gates 10492* (MBG); L'Anse Co., July, 1892, *Eby* (MBG); Keweenaw Peninsula, Aug. 1878, *Engelmann* (MBG).

Wisconsin: La Pointe, Sept. 3, 1878, *Engelmann* (MBG).

IRIS VIRGINICA L.

Specimens examined:

United States:

District of Columbia: Alexander Is., May 15, 1915, *Van Eseltine 366* (US).

Virginia: Norfolk Co., May 11, 1898, *Kearney 1079* (US); exact locality and date lacking, *Clayton 259* (BM).

North Carolina: Hendersonville, wet meadows, May 26, 1898, *Biltmore Herb. 542b* (MBG, US); Roandale Farm, June 8, 1895, *Wetherby 1067* (US).

South Carolina: Cat Island, Georgetown Co., Aug. 16, 1915, *Alexander 111* (US, NY).

Ohio: Middleburg, Cuyahoga Co., June 20, 1897, *Watson*

(MBG); Clare, Hamilton Co., spring-fed swamp, May 30, 1906, *Braun* (MBG).

KENTUCKY: Elizabethtown, May 23, 1926, *Anderson & Woodson 38* (MBG); exact locality and date lacking, *Short* (MBG); Bowling Green, swamp, May 21, 1897, *Price* (MBG); Drake's Creek, Warren Co., May, 1891, *Price* (MBG); Livermore, McLean Co., June 2, 1920, *E. J. Palmer 17707* (MBG); Ohio City, swamp, June 5, 1901, *Price* (MBG); Clay City, May 23, 1903, *Biltmore Herb. 542* (US).

TENNESSEE: Stanton, May 20, 1926, *Anderson & Woodson 60* (MBG); Knoxville, wet ground, May 1896, *Ruth* (MBG).

GEORGIA: McQueen Is., Chatham Co., brackish marshes, April 30, 1904, *Harper 2180* (MBG).

FLORIDA: Lake City, May 23, 1897, *MacKenzie* (MBG).

MICHIGAN: Adrian, June 24, 1901, *Dewey 508* (US); Ann Arbor, June 10, 1884, *Sudworth 50* (US); Flint, swamp, June 18, 1923, *Anderson* (MBG).

INDIANA: Terre Haute, May 19, 1889, *Evermann* (US); Roby, June 18, 1910, *Lansing 2789* (US); Miller's, May 30, 1902, *Chase 1799* (US).

ALABAMA: White River marshes, April 14, 1898, *Mohr* (US); Hollywood, May 15, 1902, *Biltmore Herb. 542g* (US); Pearlington, April 8, 1880, *Mohr* (US); Mobile, May 16, 1893, *Mohr* (US).

ILLINOIS: Spoon River, Stark Co., June 9, 1907, *Chase 1425* (US); Macon Co., June 12, 1915, *Clokey 2433* (US); Morgan Park Ridge, May 27, 1907, *Dixon & Gage 702* (US); Kankakee, May 27, 1913, *Crampton 124* (US); Decatur Co., May 29, year lacking, *Clokey* (MBG); French Village, St. Clair Co., May 27, 1903, *Eggert* (MBG); Olney, April 14, 1921, *Ridgway 1381* (MBG); Fish Lake, St. Clair Co., July 16, 1858, Norton (MBG); Woodlawn, Jefferson Co., May 16, 1898, *Eggert* (MBG); Decatur, date lacking, *Clokey 2789* (MBG); Shawneetown, swampy borders of lake, June 19, 1919, *E. J. Palmer 15554* (MBG); Reevesville, Johnson Co., low swampy open ground, June 3, 1919, *E. J. Palmer 15350* (MBG); Mounds, Pulaski Co., May 7, 1919, *E. J. Palmer 15074* (MBG).

MISSISSIPPI: Beauvoir, March 28, 1898, *Tracy 4463* (MBG).

MINNESOTA: Nicollet, June, 1892, *Ballard* (US); Swan Lake,

July 16, 1917, *Metcalf 40* (US); Fort Snelling, June 22, 1888, *Forwood* (US).

Iowa: Tiffin, June 5, 1909, *Somes 3132* (US); Fayette Co., June 5, 1894, *Fink 37* (US); Hamilton Co., July 1891, *Rolfs* (MBG); Missouri Valley, June 21, 1897, *Pammel 587* (MBG); Iowa City, date lacking, *Hitchcock* (MBG); Armstrong, Emmet Co., June 18, 1897, *Cratty* (MBG); Ames, June 21, 1897, *Ball & Meeker 524* (MBG).

Missouri: St. Louis Co., June 1912, *Craig* (MBG); Oakwood, Ralls Co., open woods, June 19, 1917, *Davis 7553* (MBG); Randolph, May 18, 1895, *Mackenzie 544* (MBG); Jackson Co., low wet ground, common, June 17, 1892, *Bush 1475* (MBG); Jefferson City, June 1870, *Krause* (MBG); Carthage, swamps, May 27, 1906, *E. J. Palmer 883* (MBG); Kimmswick, May 23, 1885, *Wislizenus 407* (MBG); Winfield, Lincoln Co., June 7, 1916, *Davis 1456* (MBG).

Arkansas: Nettleton, May 7, 1893, *Eggert* (MBG); Craighead, lakes, May 7, 1893, *Eggert* (MBG).

Louisiana: Hammond, April 4, 1889, *Gallup 16* (US); Minden, April 14, 1901, *Trelease* (MBG); Madisonville, May 5, 1888, *Joor* (MBG); Covington, April 1920, *Arsene 12400* (US).

Nebraska: Nebraska City, June, 1889, *Webber* (MBG).

Kansas: Wyandotte, moist places, Aug. 5, 1897, *Clothier 1067* (MBG, US).

Texas: Troupe, May 9, 1902, *Reverchon 2793* (MBG, US); Orange, April 19, 1899, *Bray 61* (US); Keechi, Leon Co., April 20, 1918, *E. J. Palmer 13420* (MBG); Beaumont, Jefferson Co., April 22, 1916, *E. J. Palmer 9522* (MBG).

III. Intra-specific Variation in Iris versicolor and Iris virginica

Wherever either species was studied, the individual plants which went to make up a colony were found to vary strikingly among themselves. They varied in every conceivable characteristic, both vegetative and floral, though the latter variations were the most conspicuous. The flowers varied in size and form, in color and color pattern, in number and arrangement, in texture, and in odor. Plate 34 shows such of these differences as can be

Three flowers each of six plants of *Iris virginica* from Portage des Sioux, Mo.

recorded by the camera for six individuals from a typical colony, that of *Iris virginica* at Portage des Sioux, Missouri. They are not selected extremes but are the first six individuals which were located with at least three flowers apiece. The pictures were taken under uniform conditions as regards lighting, exposures, development, etc., and such differences as occur are due to differences in the color and texture of the flowers themselves. It may not be out of place to call attention to some of the differences which obtain between these six plants, since they are similar to the differences which were met with everywhere throughout the study.

Plant No. 1. Petals narrow and ruffled, ovary short.
Plant No. 2. Petals flat and wide, flower pale blue in color.
Plant No. 3. Entire plant large and robust, of great vegetative vigor, clone covering half an acre, flowers marked with dark blue veins on a light background, spot on sepal large and brilliant.
Plant No. 4. Flowers small and light colored, sepals broadly spatulate.
Plant No. 5. Flowers pale gray-blue, sepals long and narrow, stems and leaves very short, plant floriferous.
Plant No. 6. Flowers dark reddish blue, ovary short, stems slender, few-flowered.

In order to summarize and average such differences as these it becomes necessary to select a few for concentrated study. The characters chosen should fulfill three conditions; they should be easily measurable; they should show some variability; and they should not be easily affected by environmental influences. The first qualification eliminates a number of very conspicuous differences, such as color and color pattern, which are not adapted to quick and accurate measurement. The second bars those characters, such as the length of the anther, which are practically indentical for a large number of species of *Iris*. All of the characteristics of the plant are, of course, open to the objection that they are affected by the environment but some of them are much more stable than others. The leaf characters are particularly poor. The largest leaf on a plant may be two or three times

as wide as the smallest. The size and shape of the seed capsules are likewise extremely variable on the same plant in different seasons and under different conditions. In general the dimensions of the floral elements are less easily affected, and since they are of predominant importance from a taxonomic standpoint they were very largely used in the present work.

After a year's preliminary study, seven characters were chosen for measurement and have been used throughout the work. Five others were subsequently tried extensively, and three of these are being used at the present time. The characters chosen and the exact manner in which measurements were taken are shown in fig. 5.

These characters are measured as follows:

Sepal length. This is the maximum length of the sepal from the base of the stamen to the tip.

Sepal width. The maximum width at right angles to the length.

Sepal taper. Distance from the tip to the point of maximum width.

Petal length. Unfortunately there was no exact lower boundary as in the case of the sepal, and some of the variation in the earlier measurements is due to the fact that different points were used as a base. It was eventually defined as the line between the bases of the lateral flanges at which it breaks off naturally when pulled over backward.

Petal width. The maximum width at right angles to the length.

Petal taper. The distance from the tip to the point of maximum width.

Crest. The maximum length of the appendages of the stigma, measured from their tips to a line connecting the ends of the stigmatic lip.

Ovary. The junction of the ovary and pedicel is distinct in both species; that between the ovary and the tube is much less so, being marked by a vague ridge. The summit of this ridge is taken as the line of demarcation and the ovary is measured from it to the base.

Tube. The tube is measured from the same point to the base of the stamen, one sepal having been removed.

Stamen. The length of the anther from the attachment of the filament to the tip.

Care was taken to measure only fully opened, uninjured flowers. Not more than one flower of a clone was measured (except in those few cases where intra-clonal variation was being studied). It was found upon experiment that one single set of measurements gave almost as consistent results as when *two* sepals and *two* petals were measured on each plant. An experiment was made on the

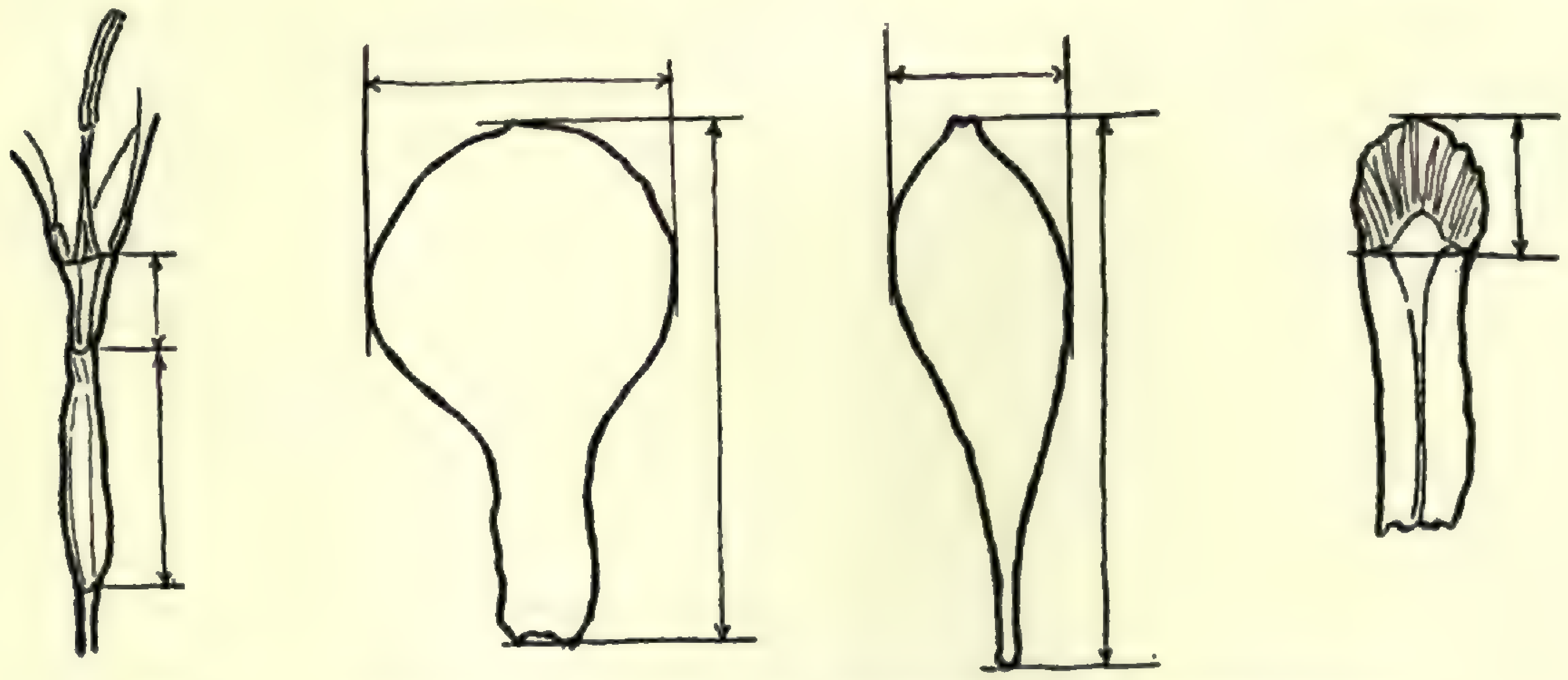


Fig. 5. Diagram showing how floral elements of *Iris* were measured.

colony at Portage des Sioux, Missouri, to determine if the measurements were being affected by the flowers not being fully expanded. Twenty flowers were measured at four o'clock in the afternoon and remeasured at seven the next morning with practically identical results.

The first five year's measurements have been summarized in tables I–IV. The figures in italics are the class containing the median or mid value. The median has been used as an average rather than the mathematical mean, since it is less influenced by occasional extreme values. The extra-small size of a frost-bitten or insect-mutilated petal, for instance, is not really significant, yet a single such extreme observation might seriously influence the position of the mathematical mean. It would have no more effect on the position of the median than would any petal of less than average size.

One fact is immediately apparent from an inspection of the summary. No single measurement will serve as a criterion for

TABLE I

IRIS VIRGINICA

Year	Town	State	Individuals of each colony classified according to size																										
			Petal length in centimeters														Total number	Sepal length in centimeters												Total Number
			1.9–2.2	2.3–2.6	2.7–3.0	3.1–3.4	3.5–3.8	3.9–4.2	4.3–4.6	4.7–5.0	5.1–5.4	5.5–5.8	5.9–6.2	6.3–6.6	6.7–7.0	7.1–7.4		3.7–4.0	4.1–4.4	4.5–4.8	4.9–5.2	5.3–5.6	5.7–6.0	6.1–6.4	6.5–6.8	6.9–7.2	7.3–7.6	7.7–8.0	8.1–8.4	
1927	Kimborough	Ala.								7	5	8*	5				25					4	6	*3*	8	3		1		25
1927	Wiggins	Miss.							1		2	4	4		1		12						3		*6*	1	1	1		12
1927	Jackson	Miss.							8	*5*	5	2	1				21				2	7	*3*	3	5	1				21
1926	Arlington	Tenn.								7	*6*	2	1	1			17					6	*5*	3	2	1				17
1926	Huntingdon	Tenn.							2	1	2	2					7					1	1	2	1	2				7
1926	Camden	Tenn.							1	8	13	*15*	7	3	3		50				1	1	7	15	*11*	7	3	5		50
1926	Bonnieville	Ky.							1		8	*11*	11	4			35					1	5	8	*8*	9	3	1		35
1926	Elizabethtown	Ky.							1	1	3	3	3				11					1	1	1	6	2				11
1926	Stanton	Ky.						1	8	*8*	3	1					21			1	4	*7*	6	3						21
1926	Hayden	Ind.						2	2	*5*	4	3	1				17				2	5	*5*	6	1					19
1926	Anna	Ill.						2	6	*16*	5	8	1	1			39				2	4	8	*14*	8	2				38
1925	Vulcan	Ill.						1	3	4	*7*	6	5				26			1	2	2	7	*8*	2	3	2			27
1926	Vulcan	Ill.						1		4	*5*	5					15					1	3	*8*	2	1				15
1924	East St. Louis	Ill.							2	3	6	*8*	4				23			1		2	2	*8*	4	3	1			21
1925	Farmington	Ark.							4	2	*14*	8	9	1			38					6	7	*10*	7	6	1	1		38
1926	Pilot Knob	Mo.								2		4	1	1			8						2	2		3	1			8
1925	Wicks	Mo.					2	10	*10*	10	8	3					43			1	6	13	*8*	8	5	2				43
1926	Valley Park	Mo.						1	1	*11*	7	2					22			1		1	*10*	7	2	1			1	23
1925	P. des Sioux	Mo.							5	1							6				1	1	2	1	1					6
1926	P. des Sioux	Mo.					3	7	9	*11*	6	3	1				40			2	3	13	*10*	5	7					40
1927	P. des Sioux	Mo.							1	9	6	*8*	6	3			33						10	*8*	3	5	3	1		30
1927	P. des Sioux	Mo.								4	9	*6*	6		2		27						7	6	*10*	4	1			28
1924	Louisiana	Mo.						1	2	*12*	9	2					26					2	8	*9*	7	1				27
1928	Rich-Tex.	S. C.											1				1										1			1
1928	Eastover	S. C.							1	1	7	*6*		4	1		20						3	5	*3*	3	5		1	20

* The figures in italics are the class containing the median or mid value.

TABLE I (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Individuals of each colony classified according to size																										
			Petal length in centimeters														Total number	Sepal length in centimeters												Total Number
			1.9–2.2	2.3–2.6	2.7–3.0	3.1–3.4	3.5–3.8	3.9–4.2	4.3–4.6	4.7–5.0	5.1–5.4	5.5–5.8	5.9–6.2	6.3–6.6	6.7–7.0	7.1–7.4		3.7–4.0	4.1–4.4	4.5–4.8	4.9–5.2	5.3–5.6	5.7–6.0	6.1–6.4	6.5–6.8	6.9–7.2	7.3–7.6	7.7–8.0	8.1–8.4	
1928	Fair Bluff	N. C.	...	...	...	...	...	...	...	...	1	3	1	...	...	...	5	...	...	...	...	...	...	...	*3*	2	...	...	...	5
1928	Wilmington	N. C.	...	...	...	...	...	...	1	...	...	2	*7*	4	2	2	18	...	...	...	...	...	1	0	3	4	*6*	2	1	17
1928	Maysville	N. C.	...	...	...	...	...	...	...	2	2	2	*7*	1	1	...	15	...	...	...	...	...	...	...	6	1	*5*	3	...	15
1928	Wolf Creek	Tenn.	...	...	...	...	...	...	...	...	...	1	...	...	...	...	1	...	...	...	...	...	...	...	...	1	...	...	...	1
1924	Fort Madison	Iowa	...	...	...	...	2	2	*9*	7	4	1	1	...	...	...	26	...	...	...	4	5	*7*	5	5	...	...	...	...	26
1924	Burk	Iowa	...	...	...	...	...	...	4	2	2	...	...	...	...	...	8	...	...	...	...	2	3	2	1	...	...	...	...	8
1924	Gilbertville	Iowa	...	...	...	...	...	1	...	4	1	4	...	...	...	...	10	...	...	...	...	1	3	5	1	...	...	...	...	10
1927	Sunbury	Ohio	...	...	...	...	...	1	3	5	*7*	10	5	...	...	...	31	...	...	...	...	...	5	8	*5*	10	2	...	...	30
1925	Mill Creek	Ohio	...	...	...	3	9	*7*	5	3	...	1	...	...	...	...	28	1	2	7	*5*	7	3	2	1	...	...	...	...	28
1925	Huron	Ohio	...	...	...	2	3	*8*	3	5	2	...	...	...	...	...	23	...	...	3	3	*6*	4	2	4	1	...	...	...	23
1925	Bay Bridge	Ohio	...	...	...	4	16	*24*	14	4	...	...	...	...	...	...	62	...	4	11	*21*	16	10	1	...	...	...	...	...	63
1925	Catawba	Ohio	...	...	2	6	18	*17*	13	...	1	...	...	...	...	...	57	2	5	13	*17*	14	6	1	...	...	...	...	...	58
1925	S. Mid. Bass Is.	Ohio	...	...	1	3	3	*10*	1	...	...	...	...	...	...	...	18	2	1	3	3	*10*	...	...	...	...	...	...	...	19
1925	N. Mid. Bass Is.	Ohio	...	...	...	1	3	10	*11*	3	3	1	...	...	...	...	32	1	1	4	*12*	9	4	1	1	1	...	...	...	34
1925	North Bass Is.	Ohio	...	...	1	1	3	4	*11*	2	...	...	...	...	...	...	22	1	3	2	*6*	6	5	...	...	...	...	...	...	23
1924	Newport	Mich.	...	...	...	...	2	3	*4*	5	1	...	...	...	...	...	15	...	...	...	3	4	*3*	4	1	...	...	...	...	15
1924	Monroe	Mich.	...	...	...	...	...	1	4	6	1	1	...	...	...	...	13	...	...	...	...	3	6	3	1	...	...	...	...	13
1924	Brooklyn	Mich.	...	...	...	1	1	7	*8*	3	1	...	1	...	...	...	22	...	1	1	7	*7*	3	2	...	1	...	...	...	22
1926	Lawrence	Mich.	...	...	...	...	...	3	5	*12*	10	4	1	...	...	...	35	...	...	...	2	7	*8*	8	4	1	...	...	...	30
1926	Colon	Mich.	...	...	...	...	...	1	*9*	*6*	2	1	1	...	...	...	20	...	...	...	1	6	*8*	2	1	1	1	...	...	20
1926	Centerville	Mich.	...	...	...	...	...	2	4	8	*9*	7	...	...	...	...	30	...	...	...	...	4	9	*13*	4	...	...	...	...	30
1926	Schoolcraft	Mich.	...	...	...	...	...	...	10	*10*	5	4	1	...	...	...	30	...	...	...	2	4	*6*	9	6	2	1	...	...	30
1926	Hartland	Mich.	...	...	...	...	...	3	9	*14*	8	1	...	...	...	...	35	...	...	...	3	7	*16*	6	3	...	...	...	...	35
1924	Armada	Mich.	...	...	...	...	2	*12*	8	3	...	...	...	...	...	...	25	...	...	2	3	*10*	8	2	...	...	...	...	...	25
1924	Yale	Mich.	...	...	...	...	2	10	*18*	12	3	1	...	...	...	...	46	...	2	2	9	*12*	12	5	3	...	...	...	...	45

TABLE I (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Individuals of each colony classified according to size																										
			Petal length in centimeters														Total number	Sepal length in centimeters												Total Number
			1.9–2.2	2.3–2.6	2.7–3.0	3.1–3.4	3.5–3.8	3.9–4.2	4.3–4.6	4.7–5.0	5.1–5.4	5.5–5.8	5.9–6.2	6.3–6.6	6.7–7.0	7.1–7.4		3.7–4.0	4.1–4.4	4.5–4.8	4.9–5.2	5.3–5.6	5.7–6.0	6.1–6.4	6.5–6.8	6.9–7.2	7.3–7.6	7.7–8.0	8.1–8.4	
1924	Otisville	Mich.	...	...	...	2	6	9	*13*	8	3	1	...	...	...	...	42	...	1	3	4	*20*	7	7	1	...	...	...	...	43
1926	Otisville	Mich.	...	...	...	...	...	5	*8*	3	3	...	...	...	...	...	19	...	...	1	4	*5*	9	...	...	...	...	...	...	19
1924	Fay Bridge	Mich.	...	...	...	1	1	6	...	3	2	...	...	...	...	...	13	...	...	2	5	2	3	1	...	...	...	...	...	13
1926	Frankenmuth	Mich.	...	...	...	...	...	4	11	*10*	7	3	...	...	...	...	35	...	...	3	2	9	*7*	6	6	2	...	...	...	35
1927	Frankenmuth	Mich.	...	...	...	...	...	1	8	*11*	7	3	...	...	...	...	30	...	...	...	2	10	*10*	2	4	2	...	...	...	30
1926	W. Saginaw	Mich.	...	...	...	...	...	1	2	*10*	3	...	...	...	...	...	16	...	...	...	2	2	*7*	2	3	...	...	...	...	16
1926	Linwood	Mich.	...	...	...	...	...	2	8	*15*	5	...	...	...	...	...	30	...	...	...	2	7	*8*	5	7	1	...	...	...	30
1927	Linwood	Mich.	...	...	...	...	1	2	5	*15*	1	1	...	...	...	...	25	...	...	1	3	4	*10*	4	1	1	...	1	...	25
1924	Muskegon	Mich.	...	...	...	2	5	10	*14*	10	2	1	...	...	...	...	44	...	2	1	3	*7*	11	1	...	...	...	...	...	25
1924	Albert Lea	Minn.	...	...	...	...	...	2	2	...	...	...	...	...	...	...	4	...	...	1	3	...	...	...	...	...	...	...	...	4
1924	Hayward	Minn.	...	...	...	...	...	1	6	2	1	...	...	...	...	...	10	...	...	...	2	3	3	2	...	...	...	...	...	10
1924	La Crosse	Wis.	...	...	...	1	...	8	14	*15*	9	4	1	...	...	...	52	...	1	1	3	*11*	*18*	12	2	3	...	1	...	52
1927	Pardeeville	Wis.	...	...	...	...	...	6	4	*10*	5	2	...	...	...	...	27	...	...	1	6	*10*	5	1	4	...	...	...	...	27
1924	Slinger	Wis.	...	...	...	...	1	6	7	*13*	5	1	...	...	...	...	33	...	...	3	2	5	*11*	9	2	1	...	...	...	33
1925	Pelee Is.	Ont.	...	...	...	...	...	1	1	1	...	...	...	...	...	...	3	...	...	...	1	1	2	...	1	...	...	...	...	5
1927	Kettle Point	Ont.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...

TABLE I (Continued)

IRIS VERSICOLOR

Year	Town	State	Individuals of each colony classified according to size: Petal length in centimeters														Total number	Sepal length in centimeters												Total Number
			1.9–2.2	2.3–2.6	2.7–3.0	3.1–3.4	3.5–3.8	3.9–4.2	4.3–4.6	4.7–5.0	5.1–5.4	5.5–5.8	5.9–6.2	6.3–6.6	6.7–7.0	7.1–7.4		3.7–4.0	4.1–4.4	4.5–4.8	4.9–5.2	5.3–5.6	5.7–6.0	6.1–6.4	6.5–6.8	6.9–7.2	7.3–7.6	7.7–8.0	8.1–8.4	
1927	Hood	Md.	...	...	3	6	*9*	7	1	...	...	...	...	...	...	...	26	...	...	...	4	8	*9*	6	...	...	...	...	...	27
1927	Liverpool	Pa.	...	...	...	4	3	*8*	5	...	...	...	...	...	...	...	20	...	...	...	2	3	*9*	4	4	...	...	...	...	22
1925	Harmonsburg	Pa.	...	3	3	*20*	9	8	...	...	...	...	...	...	...	...	43	2	1	2	12	*7*	6	5	...	...	...	...	...	35
1925	Meadville	Pa.	...	...	3	3	7	1	...	...	...	...	...	...	...	...	14	...	1	3	*7*	3	...	...	...	...	...	...	...	14
1925	Greenville	Pa.	1	...	2	4	4	1	1	...	...	...	...	...	...	...	13	...	1	4	2	...	1	...	...	...	...	...	...	8
1924	Conewango	N. Y.	...	...	...	1	3	*14*	4	6	1	...	...	...	...	...	29	...	...	...	3	8	*8*	9	1	...	...	...	...	29
1925	Conewango	N. Y.	...	1	4	*4*	4	3	...	...	...	...	...	...	...	...	16	...	2	3	*9*	2	...	...	...	...	...	...	...	16
1925	Cherry Cr.	N. Y.	...	...	1	4	*10*	3	...	...	...	...	...	...	...	...	18	...	3	6	*7*	3	...	...	...	...	...	...	...	19
1927	Villenova	N. Y.	...	...	...	...	7	*8*	8	2	...	...	...	...	...	...	25	...	...	...	4	9	*9*	4	1	1	...	...	...	28
1925	Hubbardsville	N. Y.	...	...	1	*17*	14	3	...	...	...	...	...	...	...	...	35	...	...	3	4	*14*	12	1	1	...	...	...	...	35
1925	Pownal	Vt.	...	1	12	*10*	3	1	...	...	...	...	...	...	...	...	27	1	3	7	*8*	7	1	...	...	...	...	...	...	27
1925	Pownal Center	Vt.	1	...	12	*19*	5	...	...	...	...	...	...	...	...	...	37	2	4	8	*17*	7	...	...	...	...	...	...	...	38
1925	Clarendon	Vt.	...	2	6	*15*	9	4	1	...	...	...	...	...	...	...	37	2	1	8	*13*	9	4	...	...	...	...	...	...	37
1926	Middlebury	Vt.	...	...	...	2	7	*7*	9	1	...	...	...	...	...	...	26	...	...	2	1	3	*11*	4	4	...	...	...	...	25
1926	New Haven Jc.	Vt.	...	...	1	5	9	*14*	3	2	...	...	...	...	...	...	34	...	...	...	5	11	*11*	4	3	...	...	...	...	34
1924	Holderness	N. H.	...	...	...	1	3	1	...	...	...	...	...	...	...	...	5	...	...	1	1	2	1	...	...	...	...	...	...	5
1927	Duxbury	Mass.	...	...	...	3	*11*	5	1	...	...	...	...	...	...	...	20	...	...	2	4	*10*	3	...	1	...	...	...	...	20
1927	Alberton	Ont.	...	...	...	3	7	*12*	3	...	...	...	...	...	...	...	25	...	...	1	5	*10*	10	...	...	...	...	...	...	26
1926	Ottawa	Ont.	...	...	...	3	7	*8*	10	2	1	...	...	...	...	...	31	...	...	...	1	6	*11*	6	8	...	...	...	...	32
1926	L. Timagami	Ont.	...	...	...	3	7	*5*	9	1	1	...	...	...	...	...	26	...	...	...	2	5	*8*	5	5	1	...	...	...	26
1927	Truro	N. S.	...	...	...	...	6	*9*	3	6	...	...	...	...	...	...	24	...	...	...	1	4	5	*7*	3	2	...	...	...	22
1927	Antigonish	N. S.	...	...	1	5	6	1	...	...	...	...	...	...	...	...	13	...	1	2	5	2	3	1	...	...	...	...	...	14
1927	Baddeck	N. S.	...	...	...	...	3	9	2	...	...	...	...	...	...	...	14	...	...	1	4	2	5	2	...	...	...	...	...	14
1927	McAdam	N. B.	...	...	...	2	2	7	2	...	...	...	...	...	...	...	13	...	...	...	...	6	4	2	1	...	...	...	...	13

TABLE I (Continued)

IRIS VERSICOLOR × I. VIRGINICA

Year	Town	State	Individuals of each colony classified according to size																										
			Petal length in centimeters														Total number	Sepal length in centimeters												Total number
			1.9–2.2	2.3–2.6	2.7–3.0	3.1–3.4	3.5–3.8	3.9–4.2	4.3–4.6	4.7–5.0	5.1–5.4	5.5–5.8	5.9–6.2	6.3–6.6	6.7–7.0	7.1–7.4		3.7–4.0	4.1–4.4	4.5–4.8	4.9–5.2	5.3–5.6	5.7–6.0	6.1–6.4	6.5–6.8	6.9–7.2	7.3–7.6	7.7–8.0	8.1–8.4	
1927	Tawas City	Mich.	...	...	...	6	3	1	1	...	...	...	...	...	...	...	11	...	...	1	5	3	1	1	...	...	...	...	...	11
1927	E. Tawas	Mich.	...	...	...	...	...	...	4	2	3	1	1	...	...	...	11	...	...	1	2	...	3	1	3	1	...	...	...	11
1927	W. St. Ignace	Mich.	...	...	...	1	3	6	*13*	6	3	3	...	...	...	...	35	...	...	...	3	5	8	*9*	5	3	3	...	...	36
1927	Engadine	Mich.	...	...	...	1	3	*10*	6	4	3	...	...	...	...	...	27	...	...	...	1	1	5	*10*	5	4	1	...	...	27
1924	W. Yale	Mich.	...	...	...	3	5	4	2	...	...	...	...	...	...	...	14	...	2	1	6	5	6	2	...	...	...	...	...	22
1927	London	Ont.	...	...	...	...	...	...	6	11	5	1	...	...	...	...	23	...	...	...	1	3	6	*10*	2	...	...	...	...	22

TABLE II

IRIS VIRGINICA

Individuals of each colony classified according to size

Petal width in centimeters

Year	Town	State	.5–.6	.7–.8	.9–1.0	1.1–1.2	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	Total number
1927	Kimborough	Ala.					1	3	*11**	5	1	2	2			25
1927	Wiggins	Miss.			2	1	3		2	2	1	1				12
1927	Jackson	Miss.					3	4	*8*	4	2					21
1926	Arlington	Tenn.				1	1	6	*7*	2						17
1926	Huntingdon	Tenn.					1	3	1	1	1					7
1926	Camden	Tenn.					1	3	12	*11*	9	11	3			50
1926	Bonnieville	Ky.					2	3	*14*	11	4	1				35
1926	Elizabethtown	Ky.				1	1		3	2	2	1	1			11
1926	Stanton	Ky.			1		4	*11*	1	2	2					21
1926	Hayden	Ind.			1	3	*5*	3	3	2						17
1926	Anna	Ill.					5	3	*18*	7	2	2	1			38
1925	Vulcan	Ill.						8	*7*	9	1					25
1926	Vulcan	Ill.				1	4	*5*	4	1						15
1924	E. St. Louis	Ill.					3	5	*8*	2	2		2			22
1925	Farmington	Ark.					1	1	4	7	*9*	11	3	2		38
1926	Pilot Knob	Mo.						1		4	1	2				8
1925	Wicks	Mo.				9	11	*9*	8	4	1			1		43
1926	Valley Park	Mo.				3	3	2	*7*	5	3					23
1925	P. des Sioux	Mo.				3	1	1								5
1926	P. des Sioux	Mo.			2	5	12	*9*	4	4	2	2				40
1927	P. des Sioux	Mo.				1	6	6	*5*	4	3	1	1		1	28
1928	P. des Sioux	Mo.				1		2	7	*6*	4	2	3	1	1	27
1924	Louisiana	Mo.			1		8	*3*	7	6	1					26
1928	Rich-Tex.	S. C.						1								1
1928	Eastover	S. C.			1		1		*8*	*8*	2					20
1928	Fair Bluff	N. C.				1	2	1	1							5

Sepal width in centimeters

Year	Town	State	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	3.1–3.2	3.3–3.4	3.5–3.6	3.7–3.8	3.9–4.0	4.1–4.2	Total number
1927	Kimborough	Ala.					2	3	7	*4*	2	5	2					25
1927	Wiggins	Miss.				2	1	2	1	4		1	1					12
1927	Jackson	Miss.				1	2	5	*3*	5	3	1	1					21
1926	Arlington	Tenn.						2	3	*10*		2						17
1926	Huntingdon	Tenn.					2		1		4							7
1926	Camden	Tenn.					1	0	6	12	*14*	9	5	1	2			50
1926	Bonnieville	Ky.							3	6	*12*	9	4	1				35
1926	Elizabethtown	Ky.						1	1	1	2	1	3	1				10
1926	Stanton	Ky.				1	4	5	*4*	3	2	2						21
1926	Hayden	Ind.			2	5	*2*	4		3	1							17
1926	Anna	Ill.					2	4	7	*10*	8	5		2				38
1925	Vulcan	Ill.				1	3	6	*6*	5	5	1						27
1926	Vulcan	Ill.						4	*4*	4	3							15
1924	E. St. Louis	Ill.				2	3	3	3	2	3	2	3					21
1925	Farmington	Ark.				1	2	2	6	4	*10*	5	1	2	4	1		38
1926	Pilot Knob	Mo.								1	3	1	2	1				8
1925	Wicks	Mo.			1	3	7	7	*10*	9	4	1	1					43
1926	Valley Park	Mo.			1	1	3	2	2	*3*	3	6	2					23
1925	P. des Sioux	Mo.							1	2		1		1				5
1926	P. des Sioux	Mo.				2	4	5	5	*13*	5	1	2	2			1	40
1927	P. des Sioux	Mo.					1	1	4	5	*6*	5	1	4		1		28
1928	P. des Sioux	Mo.						1	1	1	9	*4*	7	2	2	1		28
1924	Louisiana	Mo.				1		1	6	*7*	7	3	2					27
1928	Rich-Tex.	S. C.						1										1
1928	Eastover	S. C.				1	1	1	6	*3*	6	1	1					20
1928	Fair Bluff	N. C.					1		1	2	1							5

* The figures in italics are the class containing the median or mid-value.

TABLE II (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Individuals of each colony classified according to size: Petal width in centimeters														Sepal width in centimeters															
			.5–.6	.7–.8	.9–1.0	1.1–1.2	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	Total number	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	3.1–3.2	3.3–3.4	3.5–3.6	3.7–3.8	3.9–4.0	4.1–4.2	Total number
1928	Wilmington	N. C.	...	...	...	...	1	2	5	*4*	4	1	...	...	...	17	...	...	...	...	1	...	3	3	*6*	1	1	1	...	1	...	17
1928	Maysville	N. C.	...	...	...	...	...	1	6	*3*	2	2	1	...	...	15	...	...	...	...	...	...	...	1	4	*6*	2	2	...	...	...	15
1928	Wolf Creek	Tenn.	...	...	...	...	...	...	1	...	...	...	...	...	...	1	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1
1924	Fort Madison	Iowa	...	...	...	1	6	*7*	8	1	3	...	...	...	...	26	...	...	...	1	3	5	3	*5*	4	1	3	...	...	1	...	26
1924	Burk	Iowa	...	...	...	...	...	2	4	1	1	...	...	...	...	8	...	...	...	...	1	1	...	3	1	1	1	...	...	...	...	8
1924	Gilbertville	Iowa	...	...	...	...	5	1	1	...	2	...	...	...	...	9	...	...	...	...	...	4	2	1	2	...	1	...	...	...	...	10
1927	Sunbury	Ohio	...	...	...	1	3	1	*10*	*11*	3	...	1	...	...	30	...	...	...	...	1	2	6	4	*7*	4	4	1	1	...	...	30
1925	Mill Creek	Ohio	...	...	8	3	*6*	3	4	2	...	...	...	...	...	26	...	2	7	*5*	*4*	4	3	2	1	...	...	...	...	...	...	28
1925	Huron	Ohio	...	1	3	1	*11*	5	...	1	1	...	...	...	...	23	...	...	...	6	1	*5*	6	3	2	...	...	...	...	...	...	23
1925	Bay Bridge	Ohio	...	1	9	16	*17*	5	9	3	...	...	...	...	...	60	...	...	2	11	13	*16*	15	2	1	1	1	...	...	...	...	62
1925	Catawba	Ohio	...	1	5	18	*13*	9	6	4	1	...	...	...	...	57	...	...	2	9	12	*12*	10	6	4	3	...	...	...	...	...	58
1925	S. Mid. Bass Is.	Ohio	...	3	1	*6*	7	1	1	...	...	...	...	...	...	19	...	...	1	...	6	*3*	6	2	1	...	...	...	...	...	...	19
1925	N. Mid. Bass Is.	Ohio	...	...	1	3	7	*14*	5	1	...	...	...	...	...	31	...	...	...	1	9	5	*8*	4	4	...	...	1	...	...	...	32
1925	N. Bass Is.	Ohio	...	...	3	5	*7*	3	2	...	...	...	...	...	...	20	...	1	...	2	3	*5*	9	...	2	...	...	...	...	...	...	22
1924	Newport	Mich.	...	...	...	1	2	*6*	3	1	1	1	...	...	...	15	...	...	...	...	2	2	3	*4*	3	...	1	...	...	...	...	15
1924	Monroe	Mich.	...	...	...	...	6	1	4	1	1	...	...	...	...	13	...	...	1	...	3	3	2	2	...	...	2	...	...	...	...	13
1924	Brooklyn	Mich.	...	...	...	2	7	*5*	4	1	2	1	...	...	...	22	...	...	...	1	2	4	*4*	*6*	2	3	...	...	...	...	...	22
1926	Lawrence	Mich.	...	...	...	...	1	9	6	*13*	4	1	1	...	...	35	...	...	...	2	1	4	8	*8*	8	2	2	...	...	...	...	35
1926	Colon	Mich.	...	...	...	2	4	8	5	1	...	...	...	...	...	20	...	...	...	...	3	5	*5*	4	1	2	...	...	...	...	...	20
1926	Centerville	Mich.	...	...	...	2	3	9	*10*	3	1	2	...	...	...	30	...	...	...	...	...	2	8	*7*	8	3	...	2	...	...	...	30
1926	Schoolcraft	Mich.	...	...	3	...	2	6	*11*	6	2	...	...	...	...	30	...	...	...	1	4	5	*6*	6	6	2	...	...	...	...	...	30
1926	Hartland	Mich.	...	...	...	1	2	7	*10*	8	4	3	...	...	...	35	...	...	...	1	3	7	5	*10*	6	1	1	1	...	...	...	35
1924	Armada	Mich.	...	...	...	3	*11*	5	6	1	...	...	...	...	...	26	...	...	...	3	*10*	4	6	1	1	...	...	...	...	...	...	25
1924	Yale	Mich.	...	...	...	1	9	*12*	*12*	7	2	1	...	...	...	44	...	...	1	5	13	*12*	6	4	2	2	...	...	...	...	...	45
1924	Otisville	Mich.	...	...	1	3	15	*11*	10	1	1	...	...	...	...	42	...	...	2	6	12	*9*	9	4	1	...	...	...	...	...	...	43
1926	Otisville	Mich.	...	...	...	...	2	6	*6*	5	2	...	...	...	...	21	...	...	...	2	5	*5*	5	4	...	...	...	...	...	...	...	21
1924	Fay Bridge	Mich.	...	...	...	1	5	2	2	2	...	...	...	...	...	12	...	...	...	...	4	6	3	...	...	...	...	...	...	...	...	13

TABLE II (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Individuals of each colony classified according to size: Petal width in centimeters .5–.6	.7–.8	.9–1.0	1.1–1.2	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	Total number	Sepal width in centimeters 1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	3.1–3.2	3.3–3.4	3.5–3.6	3.7–3.8	3.9–4.0	4.1–4.2	Total number
1926	Frankenmuth	Mich.	...	...	...	3	2	4	*14*	9	1	1	...	1	...	35	...	...	...	3	2	9	*6*	8	3	2	2	...	...	...	...	35
1927	Frankenmuth	Mich.	...	...	...	1	2	8	*10*	6	2	1	...	...	...	30	...	1	...	2	1	3	6	*8*	7	2	...	...	...	...	...	30
1926	W. Saginaw	Mich.	...	...	...	...	...	1	4	*7*	3	1	...	...	...	16	...	...	...	...	1	3	3	*3*	4	2	...	...	...	...	...	16
1926	Linwood	Mich.	...	...	...	1	3	3	*8*	*9*	5	1	...	...	...	30	...	...	...	1	1	2	5	*6*	*7*	5	2	1	...	...	...	30
1927	Linwood	Mich.	...	...	...	1	2	8	*3*	5	2	4	...	...	...	25	...	...	...	1	1	2	2	6	*3*	4	3	2	1	...	...	25
1924	Muskegon	Mich.	...	...	...	2	9	*16*	8	4	2	3	...	...	...	44	...	4	...	4	11	*10*	4	6	2	1	1	...	...	...	...	43
1924	Albert Lea	Minn.	...	...	...	...	...	3	1	...	...	...	...	...	...	4	...	...	...	1	2	1	...	...	...	...	...	...	...	...	...	4
1924	Hayward	Minn.	...	...	...	1	4	3	1	...	...	...	...	...	...	9	...	...	1	...	4	4	...	1	...	...	...	...	...	...	...	10
1924	La Crosse	Wis.	...	...	...	7	7	*16*	11	6	4	1	...	...	...	52	...	...	...	...	1	11	*15*	8	6	9	2	...	...	...	...	52
1927	Pardeeville	Wis.	...	...	...	...	...	7	*10*	6	4	...	...	...	...	27	...	...	...	...	2	6	3	*5*	7	1	3	...	...	...	...	27
1924	Slinger	Wis.	...	...	...	2	2	9	*12*	2	4	2	...	...	...	33	...	...	...	2	7	*10*	3	6	4	1	...	...	...	...	...	33
1925	Pelee Is.	Ont.	...	...	...	...	1	1	...	2	...	...	...	...	...	4	...	...	...	...	...	...	1	1	2	...	...	...	...	...	...	4
1927	Kettle Point	Ont.	...	...	...	...	...	...	...	...	...	...	...	...	...	.....	...	...	...	...	...	1	...	...	1	1	...	...	...	...	...	3

TABLE II (Continued)

IRIS VERSICOLOR

Individuals of each colony classified according to size

Petal width in centimeters

Year	Town	State	.5–.6	.7–.8	.9–1.0	1.1–1.2	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	Total number
1927	Hood	Md.	1	3	8	*6*	5	2	1	...	...	...	...	...	...	26
1927	Liverpool	Pa.	...	1	3	3	*5*	6	1	1	...	...	...	...	...	20
1925	Harmonsburg	Pa.	...	6	4	*12*	8	3	...	...	...	...	...	...	...	33
1925	Meadville	Pa.	...	9	4	1	...	...	...	...	...	...	...	...	...	14
1925	Greenville	Pa.	...	3	7	1	...	...	...	...	...	...	...	...	...	11
1924	Conewango	N. Y.	...	...	...	2	4	6	*6*	9	2	...	...	...	...	29
1925	Conewango	N. Y.	...	2	5	*4*	4	1	...	...	...	...	...	...	...	16
1925	Cherry Cr.	N. Y.	...	3	5	*5*	2	3	...	...	...	...	...	...	...	18
1927	Villenova	N. Y.	...	...	...	...	6	*9*	9	2	...	...	...	...	...	26
1925	Hubbardsville	N. Y.	...	5	*13*	10	5	1	...	...	...	...	...	...	...	34
1925	Pownal	Vt.	1	10	*11*	2	2	...	...	...	...	...	...	...	...	26
1925	Pownal Cent.	Vt.	...	11	*8*	*11*	7	...	1	...	...	...	...	...	...	38
1925	Clarendon	Vt.	...	4	*15*	13	3	1	...	...	...	...	...	...	...	36
1926	Middlebury	Vt.	...	...	...	4	*10*	5	4	2	...	...	...	...	...	25
1926	New Haven Jct.	Vt.	...	...	3	5	*9*	*8*	6	2	1	...	...	...	...	34
1924	Holderness	N. H.	...	1	2	2	...	...	...	...	...	...	...	...	...	5
1927	Duxbury	Mass.	...	...	1	8	*7*	1	...	2	...	1	...	...	...	20
1927	Alberton	Ont.	...	...	...	1	5	*8*	9	1	1	...	...	...	...	25
1926	Ottawa	Ont.	...	...	3	10	*7*	7	3	...	...	1	...	...	...	31
1926	L. Timagami	Ont.	...	...	4	*10*	9	2	1	...	...	...	...	...	...	26
1927	Truro	N. S.	...	...	1	4	*10*	5	...	3	...	...	...	...	...	23
1927	Antigonish	N. S.	...	...	...	2	6	4	1	...	...	...	...	...	...	13
1927	Baddeck	N. S.	...	...	...	7	1	2	4	1	...	...	...	...	...	15
1927	McAdam	N. B.	...	...	1	1	2	3	3	1	1	...	...	...	...	12

Sepal width in centimeters

Year	Town	State	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	3.1–3.2	3.3–3.4	3.5–3.6	3.7–3.8	3.9–4.0	4.1–4.2	Total number
1927	Hood	Md.	...	...	...	1	2	5	4	*10*	3	1	1	...	...	...	...	27
1927	Liverpool	Pa.	...	...	...	...	1	...	1	6	*4*	6	3	...	1	...	...	22
1925	Harmonsburg	Pa.	...	...	...	2	1	3	10	*11*	6	1	...	...	...	...	...	34
1925	Meadville	Pa.	...	...	1	...	4	3	4	1	...	...	...	...	...	...	...	13
1925	Greenville	Pa.	...	...	1	1	3	2	2	3	...	1	...	...	...	...	...	13
1924	Conewango	N. Y.	...	...	...	...	1	...	1	1	6	*10*	7	3	...	...	...	29
1925	Conewango	N. Y.	...	...	...	1	2	2	*6*	3	1	...	...	...	...	...	...	15
1925	Cherry Cr.	N. Y.	...	...	...	1	1	3	*8*	3	2	1	...	...	...	...	...	19
1927	Villenova	N. Y.	...	...	...	...	...	2	4	6	*10*	2	1	...	...	1	...	26
1925	Hubbardsville	N. Y.	...	...	...	1	5	4	*8*	3	10	2	2	...	...	...	...	35
1925	Pownal	Vt.	...	...	2	6	*7*	8	3	1	...	...	...	...	...	...	...	27
1925	Pownal Cent.	Vt.	...	...	3	7	4	*11*	6	5	1	...	...	...	...	...	...	37
1925	Clarendon	Vt.	...	...	1	1	4	12	*8*	8	3	...	...	...	...	...	...	37
1926	Middlebury	Vt.	...	...	...	...	1	3	3	4	*8*	3	1	2	...	...	...	25
1926	New Haven Jct.	Vt.	...	...	...	...	1	2	4	5	*8*	8	4	2	...	...	...	34
1924	Holderness	N. H.	...	...	...	1	1	...	1	1	1	...	...	...	...	...	...	5
1927	Duxbury	Mass.	...	...	...	...	1	...	3	*8*	3	3	1	1	...	...	...	20
1927	Alberton	Ont.	...	...	...	...	...	2	1	7	*5*	6	3	1	1	...	...	26
1926	Ottawa	Ont.	...	...	...	...	...	3	6	5	*6*	4	3	2	3	...	...	32
1926	L. Timagami	Ont.	...	...	...	...	...	...	2	3	5	*10*	3	2	1	...	...	26
1927	Truro	N. S.	...	...	...	...	...	1	4	*9*	3	2	3	1	...	...	...	23
1927	Antigonish	N. S.	...	...	...	...	...	...	4	1	4	3	2	...	...	...	...	14
1927	Baddeck	N. S.	...	...	...	...	...	2	4	3	5	...	...	...	...	...	...	14
1927	McAdam	N. B.	...	...	...	...	...	1	...	2	5	2	...	1	1	...	...	12

TABLE II (Continued)

IRIS VERSICOLOR × I. VIRGINICA

Year	Town	State	Individuals of each colony classified according to size: Petal width in centimeters													Total number	Sepal width in centimeters															Total number
			.5–.6	.7–.8	.9–1.0	1.1–1.2	1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0		1.3–1.4	1.5–1.6	1.7–1.8	1.9–2.0	2.1–2.2	2.3–2.4	2.5–2.6	2.7–2.8	2.9–3.0	3.1–3.2	3.3–3.4	3.5–3.6	3.7–3.8	3.9–4.0	4.1–4.2	
1927	Tawas City	Mich.	...	...	...	6	2	1	2	...	...	...	...	...	...	11	...	...	...	...	...	2	4	2	3	...	...	...	...	...	...	11
1927	E. Tawas	Mich.	...	...	...	...	...	3	2	6	...	...	...	...	...	11	...	...	...	1	...	2	3	2	3	...	...	...	...	...	...	11
1924	W. St. Ignace	Mich.	...	...	3	4	*11*	8	4	4	1	...	...	...	...	35	...	...	...	2	3	2	6	*5*	8	6	1	1	1	...	...	35
1927	Engadine	Mich.	...	...	...	4	5	*8*	5	3	1	1	...	...	...	27	...	...	...	...	...	...	1	3	3	*8*	4	3	5	...	...	27
1927	W. Yale	Mich.	...	1	5	1	6	1	...	...	...	...	...	...	...	14	...	...	...	...	3	3	*4*	2	1	...	2	...	...	...	...	15
1927	London	Ont.	...	...	...	...	...	3	*9*	10	1	...	...	...	...	23	...	...	...	...	...	3	4	*5*	4	6	1	...	...	...	...	23

TABLE III

IRIS VIRGINICA

Year	Town	State	Individuals of each colony classified according to size																								
			Petal taper in centimeters												Total number	Sepal taper in centimeters										Total number
			.6–.7	.8–.9	1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9		1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9	
1927	Kimborough	Ala.	...	...	3	4	4	*5**	6	3	...	...	...	...	25	...	1	3	4	*4*	11	2	...	...	...	25
1927	Wiggins	Miss.	...	...	...	1	1	2	4	3	...	...	1	...	12	...	...	...	...	2	1	4	2	1	1	11
1927	Jackson	Miss.	...	...	3	5	2	*5*	3	2	1	...	...	...	21	...	2	1	5	*4*	3	4	...	1	1	21
1926	Arlington	Tenn.	...	...	2	...	5	*4*	3	2	1	...	...	...	17	...	...	...	3	5	*3*	2	2	...	2	17
1926	Huntingdon	Tenn.	...	...	2	...	1	2	1	1	...	...	...	...	7	...	...	1	1	1	...	2	1	1	...	7
1926	Camden	Tenn.	...	...	3	3	15	*9*	9	7	2	1	1	...	50	...	1	1	5	5	*14*	12	8	3	1	50
1926	Bonnieville	Ky.	...	1	...	5	5	*10*	4	8	1	1	...	...	35	...	...	2	1	5	8	*9*	9	1	...	35
1926	Elizabethtown	Ky.	...	...	...	1	5	2	3	...	...	...	...	...	11	...	...	2	...	1	6	1	...	1	...	11
1926	Stanton	Ky.	...	2	*11*	2	3	2	1	...	...	...	...	...	21	4	3	*7*	5	...	2	...	...	...	...	21
1926	Hayden	Ind.	...	...	3	3	*7*	2	1	1	...	...	...	...	17	...	4	5	3	3	...	2	...	...	...	17
1926	Anna	Ill.	...	...	5	8	*14*	6	3	...	1	...	...	...	37	...	...	2	5	11	*15*	3	2	...	...	38
1925	Vulcan	Ill.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	Vulcan	Ill.	...	...	1	3	*6*	3	1	1	...	...	...	...	15	...	1	2	*7*	2	3	...	...	...	...	15
1924	E. St. Louis	Ill.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Farmington	Ark.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	Pilot Knob	Mo.	...	...	...	...	1	2	1	1	1	...	...	...	6	...	...	...	1	2	1	2	2	...	...	8
1925	Wicks	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	Valley Park	Mo.	...	...	1	5	*5*	*4*	5	...	2	...	...	...	22	...	1	1	4	*7*	6	2	...	1	1	23
1925	P. des Sioux	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	P. des Sioux	Mo.	...	2	5	*14*	14	1	3	1	...	...	...	...	40	...	1	5	8	*13*	8	3	1	1	...	40
1927	P. des Sioux	Mo.	...	...	1	4	6	*6*	3	4	1	2	...	1	28	...	...	2	6	*6*	5	4	3	1	...	27
1924	Louisiana	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Fort Madison	Iowa	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Burk	Iowa	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—

* The figures in italics are the class containing the median or mid value.

TABLE III (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Individuals of each colony classified according to size																							
			Petal taper in centimeters												Total number	Sepal taper in centimeters										Total number
			.6–.7	.8–.9	1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9		1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9	
1924	Gilbertville	Iowa	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1927	Sunbury	Ohio	...	1	6	*9*	8	6	...	...	...	...	...	...	30	...	2	9	3	*10*	6	...	...	...	...	30
1925	Mill Creek	Ohio	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Huron	Ohio	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Bay Bridge	Ohio	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Catawba	Ohio	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	S. Middle Bass Is.	Ohio	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	N. Middle Bass Is.	Ohio	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	North Bass Is.	Ohio	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Newport	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Monroe	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Brooklyn	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	Lawrence	Mich.	...	1	1	12	*10*	8	2	1	...	...	...	...	35	...	3	6	*10*	9	6	1	...	...	...	35
1926	Colon	Mich.	...	3	5	*6*	4	...	2	...	...	...	...	...	20	1	5	*7*	2	2	2	1	...	...	...	20
1926	Centerville	Mich.	1	2	5	*8*	7	5	2	...	...	...	...	...	30	...	3	5	*7*	*12*	2	1	...	...	...	30
1926	Schoolcraft	Mich.	...	1	10	*6*	8	3	1	1	...	...	...	...	30	...	6	8	*7*	5	4	...	...	...	...	30
1926	Hartland	Mich.	...	2	3	10	*14*	5	1	...	...	...	...	...	35	...	5	10	*11*	7	2	...	...	...	...	35
1924	Armada	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Yale	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Otisville	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	Otisville	Mich.	...	2	6	*9*	1	3	...	...	...	...	...	...	21	2	5	*7*	4	...	...	...	...	...	...	18
1924	Fay Bridge	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	Frankenmuth	Mich.	...	1	7	*12*	8	5	...	2	...	...	...	...	35	2	4	*12*	7	7	3	...	...	...	...	35
1927	Frankenmuth	Mich.	...	2	4	6	*5*	6	4	1	2	...	...	...	30	...	2	11	*10*	7	...	...	...	...	...	30
1926	W. Saginaw	Mich.	...	...	1	5	*5*	4	1	...	...	...	...	...	16	...	1	*8*	2	3	2	...	...	...	...	16

TABLE III (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Individuals of each colony classified according to size: Petal taper in centimeters													Sepal taper in centimeters										
			.6–.7	.8–.9	1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9	Total number	1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9	Total number
1926	Linwood	Mich.	1	...	3	9	*11*	4	1	...	...	...	...	...	29	...	4	5	*10*	5	3	2	1	...	...	30
1927	Linwood	Mich.	...	...	...	8	*13*	3	...	1	...	...	...	...	25	...	1	2	8	*9*	1	3	1	...	...	25
1924	Muskegon	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Albert Lea	Minn.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Hayward	Minn.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	La Crosse	Wis.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1927	Pardeeville	Wis.	...	...	6	*13*	4	3	1	...	...	...	...	...	27	...	1	6	*10*	7	3	...	...	...	...	27
1924	Slinger	Wis.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Pelee Is.	Ont.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1927	Kettle Point	Ont.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	1	...	...	1	...	...	...	3

TABLE III (Continued)

IRIS VERSICOLOR

Year	Town	State	Individuals of each colony classified according to size																							
			Petal taper in centimeters												Total number	Sepal taper in centimeters										Total number
			.6–.7	.8–.9	1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9		1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9	
1927	Hood	Md.	...	7	*13*	5	1	...	...	...	...	...	...	...	26	...	1	3	7	*10*	4	2	...	...	...	27
1927	Liverpool	Pa.	...	...	3	*8*	7	1	1	...	...	...	...	...	20	...	...	...	...	3	7	*9*	2	...	...	21
1925	Harmonsburg	Pa.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Meadville	Pa.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Greenville	Pa.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1924	Conewango	N. Y.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Conewango	N. Y.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Cherry Creek	N. Y.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1927	Villenova	N. Y.	...	...	2	9	*9*	5	1	...	...	...	...	...	26	...	...	...	3	4	*12*	5	2	...	...	26
1925	Hubbardsville	N. Y.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Pownal	Vt.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Pownal Cent.	Vt.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1925	Clarendon	Vt.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1926	Middlebury	Vt.	...	...	4	*10*	7	4	...	...	...	...	...	...	25	...	...	2	2	2	6	*6*	4	3	...	25
1926	New Haven Jct.	Vt.	...	...	4	*14*	13	2	1	...	...	...	...	...	34	...	...	...	1	13	*6*	7	6	1	...	34
1924	Holderness	N. H.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1927	Duxbury	Mass.	...	...	4	*11*	2	1	1	1	...	...	...	...	20	...	1	2	3	3	*5*	4	2	...	...	19
1927	Alberton	Ont.	...	...	4	*11*	8	2	...	...	...	...	...	...	25	...	...	2	4	6	*12*	1	1	...	...	26
1926	Ottawa	Ont.	...	1	4	7	*7*	10	2	...	...	...	...	...	31	...	...	1	2	6	*10*	8	3	...	2	32
1926	L. Timagami	Ont.	...	...	3	*11*	9	1	1	1	...	...	...	...	26	...	...	...	4	5	*4*	*6*	5	2	...	26
1927	Truro	N. S.	...	...	...	2	8	*6*	4	4	...	...	...	...	24	...	...	...	3	7	*7*	4	2	...	...	23
1927	Antigonish	N. S.	...	1	3	7	2	...	...	...	...	...	...	...	13	...	...	...	5	4	2	3	...	...	...	14
1927	Baddeck	N. S.	...	...	1	3	7	2	2	...	...	...	...	...	15	1	...	1	3	6	3	...	...	...	...	14
1927	McAdam	N. B.	...	1	2	2	5	2	...	...	...	...	...	...	12	...	...	...	2	4	6	...	...	...	...	12

TABLE III (Continued)

IRIS VERSICOLOR × I. VIRGINICA

Year	Town	State	Individuals of each colony classified according to size: Petal taper in centimeters												Total number	Sepal taper in centimeters										Total number
			.6–.7	.8–.9	1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9		1.0–1.1	1.2–1.3	1.4–1.5	1.6–1.7	1.8–1.9	2.0–2.1	2.2–2.3	2.4–2.5	2.6–2.7	2.8–2.9	
1927	Tawas City	Mich.	1	2	6	1	1	...	...	...	...	...	...	...	11	...	...	5	2	4	...	...	...	...	...	11
1927	E. Tawas	Mich.	...	...	3	3	3	2	...	...	...	...	...	...	11	...	2	3	3	2	1	...	...	...	...	11
1927	W. St. Ignace	Mich.	...	2	3	8	*15*	5	1	1	...	...	...	...	35	...	1	4	6	7	*10*	4	2	...	1	35
1927	Engadine	Mich.	...	1	3	6	*6*	7	4	...	...	...	...	...	27	...	...	...	1	6	*12*	7	1	...	...	27
1924	W. Yale	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	...	...	...	...	...	—
1927	London	Ont.	...	...	1	8	*6*	1	4	3	...	...	...	...	23	...	1	4	5	*8*	5	...	...	...	...	23

TABLE IV

IRIS VIRGINICA

Individuals of each colony classified according to size

Year	Town	State	Anther length in centimeters															Total number
			.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	
1927	Kimborough	Ala.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1927	Wiggins	Miss.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1927	Jackson	Miss.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Arlington	Tenn.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Huntingdon	Tenn.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Camden	Tenn.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Bonnieville	Ky.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Elizabethtown	Ky.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Stanton	Ky.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Hayden	Ind.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Anna	Ill.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1925	Vulcan	Ill.	...	...	...	...	...	...	1	2	4	*11*	5	...	2	1	...	26
1926	Vulcan	Ill.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1924	E. St. Louis	Ill.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1925	Farmington	Ark.	...	...	...	...	...	...	...	2	1	5	10	*8*	4	4	3	37
1926	Pilot Knob	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1925	Wicks	Mo.	...	...	...	3	1	8	*16*	7	5	1	1	...	...	...	...	42
1926	Valley Park	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1925	P. des Sioux	Mo.	...	...	...	...	...	1	...	3	1	5	...	...	...	...	...	10
1926	P. des Sioux	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1927	P. des Sioux	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1924	Louisiana	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1928	Rich-Tex	S. C.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1928	Eastover	S. C.	...	...	...	...	1	2	4	*4*	1	3	4	1	...	...	...	20
1928	Fair Bluff	N. C.	...	...	...	...	1	1	1	1	1	...	...	...	...	...	...	5
1928	Wilmington	N. C.	...	...	...	...	...	1	...	1	3	2	*4*	4	...	...	1	16

Year	Town	State	Crest in centimeters														Total number
			.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	
1927	Kimborough	Ala.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1927	Wiggins	Miss.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1927	Jackson	Miss.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	Arlington	Tenn.	...	...	...	3	*6**	3	...	3	1	1	...	...	...	...	17
1926	Huntingdon	Tenn.	...	...	...	2	...	3	2	...	...	...	...	...	...	...	7
1926	Camden	Tenn.	...	...	1	2	6	7	*10*	14	7	1	...	1	1	...	50
1926	Bonnieville	Ky.	...	...	2	4	5	5	*6*	7	1	3	...	...	...	...	33
1926	Elizabethtown	Ky.	...	...	...	2	2	2	1	3	1	...	...	...	...	...	11
1926	Stanton	Ky.	...	1	1	3	4	*7*	3	...	1	...	...	...	...	...	20
1926	Hayden	Ind.	...	1	...	...	2	3	*3*	4	3	1	...	...	...	...	17
1926	Anna	Ill.	...	...	3	2	9	*7*	9	4	1	1	1	...	...	...	37
1925	Vulcan	Ill.	...	...	...	1	3	2	5	*8*	3	3	1	...	1	...	27
1926	Vulcan	Ill.	...	...	...	2	4	*4*	1	3	1	...	...	...	...	...	15
1924	E. St. Louis	Ill.	...	...	...	...	2	3	*8*	3	4	1	1	...	...	...	22
1925	Farmington	Ark.	...	...	...	...	1	3	4	*11*	7	4	3	4	...	1	38
1926	Pilot Knob	Mo.	...	...	...	...	...	1	5	...	1	1	...	...	...	...	8
1925	Wicks	Mo.	...	...	1	8	6	*7*	11	5	2	2	...	...	...	...	42
1926	Valley Park	Mo.	...	1	...	2	7	*4*	5	2	1	1	...	...	...	...	23
1925	P. des Sioux	Mo.	...	...	3	1	...	1	...	1	...	...	...	...	...	...	6
1926	P. des Sioux	Mo.	2	...	6	11	*11*	6	3	...	...	...	...	...	...	...	39
1927	P. des Sioux	Mo.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1924	Louisiana	Mo.	...	...	...	2	2	4	*9*	5	2	1	1	...	...	...	26
1928	Rich-Tex	S. C.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1928	Eastover	S. C.	...	...	2	1	1	3	3	3	4	2	...	1	...	...	20
1928	Fair Bluff	N. C.	...	...	1	...	3	...	1	...	...	...	...	...	...	...	5
1928	Wilmington	N. C.	...	...	...	3	1	1	2	2	5	3	...	...	...	...	17

* The figures in italics are the class containing the median or mid value.

TABLE IV (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Anther length in centimeters															Total number	Crest in centimeters														Total number
			.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1		.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	
1928	Maysville	N. C.							1		6	4	1	2	1			15						1	1	3	3	4	2	1			15
1928	Wolf Creek	Tenn.																					1										1
1924	Fort Madison	Iowa																				1	4	10	8	2			1				26
1924	Burk	Iowa																			2	2	3	1									8
1924	Gilbertville	Iowa																			1		1		3		3		1				9
1927	Sunbury	Ohio																															
1925	Mill Creek	Ohio						6	7	6	8		1					28	3	6	5	8	10	4	1	1							38
1925	Huron	Ohio		1	1		2	2	9	6	2							23															
1925	Bay Bridge	Ohio					3	17	8	17	8	3	2	1				59	8	7	11	16	9	7	2	1							61
1925	Catawba	Ohio			2	2	3	12	19	14	4	1			1			58	10	12	8	17	7	3									57
1925	S. Mid. Bass Is.	Ohio				1	4	5	3	5								18			1	6	9		1								17
1925	N. Mid. Bass Is.	Ohio					1	4	7	11	6	1	2					32		2	2	7	10	6	3	1							31
1925	North Bass Is.	Ohio				1		3	2	8	5	2						21	1	2	3	5	4	2	1								18
1924	Newport	Mich.																			1	3	6	4		1							15
1924	Monroe	Mich.																			1	1	4	2	1	3							12
1924	Brooklyn	Mich.																			1	4	4	10	3								22
1926	Lawrence	Mich.																			1	3	9	12	6	3	1						35
1926	Colon	Mich.																				2	7	6	1	4							20
1926	Centerville	Mich.																			2	1	6	10	3	4	1	3					30
1926	Schoolcraft	Mich.																			3	2	7	7	4	3	1	2	1				30
1926	Hartland	Mich.																				1	4	4	6	11	7		1		1		35
1924	Armada	Mich.																			1	2	16	5	1								25
1924	Yale	Mich.																		1	1	6	13	10	9	4		1					45
1924	Otisville	Mich.																		1	3	6	19	5	4	2							40
1926	Otisville	Mich.																		1	1	7	1	4	4		1						19

TABLE IV (Continued)

IRIS VIRGINICA (Continued)

Year	Town	State	Individuals of each colony classified according to size: Anther length in centimeters															Total number	Crest in centimeters														Total number
			.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1		.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	
1924	Fay Bridge	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	3	3	3	1	1	2	...	...	...	...	...	...	13
1926	Frankenmuth	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	3	4	9	*8*	4	5	1	...	...	...	...	...	35
1927	Frankenmuth	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1926	W. Saginaw	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	2	*5*	2	4	1	...	...	...	...	...	16
1926	Linwood	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	5	*10*	7	3	1	2	...	1	...	...	30
1927	Linwood	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1924	Muskegon	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	6	*14*	11	8	1	1	...	...	...	...	...	43
1924	Albert Lea	Minn.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	1	...	1	...	...	...	...	...	...	...	4
1924	Hayward	Minn.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	1	2	3	1	...	...	...	1	...	...	10
1924	La Crosse	Wis.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	3	3	12	*12*	7	5	5	2	...	...	...	51
1927	Pardeeville	Wis.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1924	Slinger	Wis.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1	6	*13*	7	3	2	...	...	...	...	...	33
1925	Pelee Is.	Ont.	...	...	...	...	...	...	4	1	...	...	...	...	...	...	...	5	...	...	...	...	2	1	...	...	1	...	...	...	...	...	4
1927	Kettle Point	Ont.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

TABLE IV (Continued)

IRIS VERSICOLOR

Year	Town	State	Individuals of each colony classified according to size: Anther length in centimeters .7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	Total number	Crest in centimeters .7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	Total number
1927	Hood	Md.																														
1927	Liverpool	Pa.																														
1925	Harmonsburg	Pa.	1	1		2	3	5	6	*15*	6	3					42	3	11	*14*	12	3										43
1925	Meadville	Pa.				1	1	1	7	2							12		1	6	2	1										10
1925	Greenville	Pa.				1		4	5	2	1						13	1	1	3	6	2										13
1924	Conewango	N. Y.																	1	1	2	5	*7*	7	3							26
1925	Conewango	N. Y.			1		3	*4*	*6*	2							16		2	3	*8*	2										15
1925	Cherry Creek	N. Y.				1	3	*7*	3	3	2						19		1	5	*8*	4	1									19
1927	Villenova	N. Y.																														
1925	Hubbardsville	N. Y.			2	4	4	*9*	8	5	2	1					35		2	6	9	*6*	9		3							35
1925	Pownal	Vt.				1	5	*12*	7	2							27	2	5	6	*10*	3	1									27
1925	Pownal Cent.	Vt.			1	16	*9*	5	3	1	1						36	3	7	*9*	*10*	8	1									38
1925	Clarendon	Vt.			2	4	9	*10*	7	3	2						37	2	5	3	*12*	12	3									37
1926	Middlebury	Vt.																			2	6	*8*	4	3	1						24
1926	New Haven Jc.	Vt.																	1	2	9	4	*9*	8	1							34
1924	Holderness	N. H.				1		2									3			1	1	1	1									4
1927	Duxbury	Mass.																														
1927	Alberton	Ont.																														
1926	Ottawa	Ont.																		1	3	11	*8*	7	1							31
1926	L. Timagami	Ont.																	1	1	4	5	*4*	4	4	2						25
1927	Truro	N. S.																														
1927	Antigonish	N. S.																														
1927	Baddeck	N. S.																														
1927	McAdam	N. B.																														

TABLE IV (Continued)

IRIS VERSICOLOR × I. VIRGINICA

Year	Town	State	Individuals of each colony classified according to size																												
			Anther length in centimeters														Total number	Crest in centimeters														Total number
			.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0		.7	.8	.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	
1927	Tawas City	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	1	3	4	3	...	...	...	...	...	...	...	11
1927	E. Tawas	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	...	3	3	3	1	1	...	...	...	...	11
1927	W. St. Ignace	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	...	5	7	7	8	5	1	2	...	...	...	35
1927	Engadine	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	1	...	1	2	7	3	10	4	...	...	...	...	28
1924	W. Yale	Mich.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	3	4	5	2	...	...	...	...	...	...	...	...	14
1927	London	Ont.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	—	...	...	...	2	4	6	4	2	2	...	...	...	...	...	20

separating the two species. It is thus apparent at the outset that no biometric method of distinguishing the two species can be a simple matter. While it is certainly true, as Hall and Clements ('23) and McLeod ('26) have suggested, that taxonomy needs the development of more exact methods, there are serious limitations to a wholesale inclusion of biometry in every-day taxonomic procedure.

These limitations may be easily demonstrated by a simple example. Figure 6 shows five petals of *Iris virginica* and five

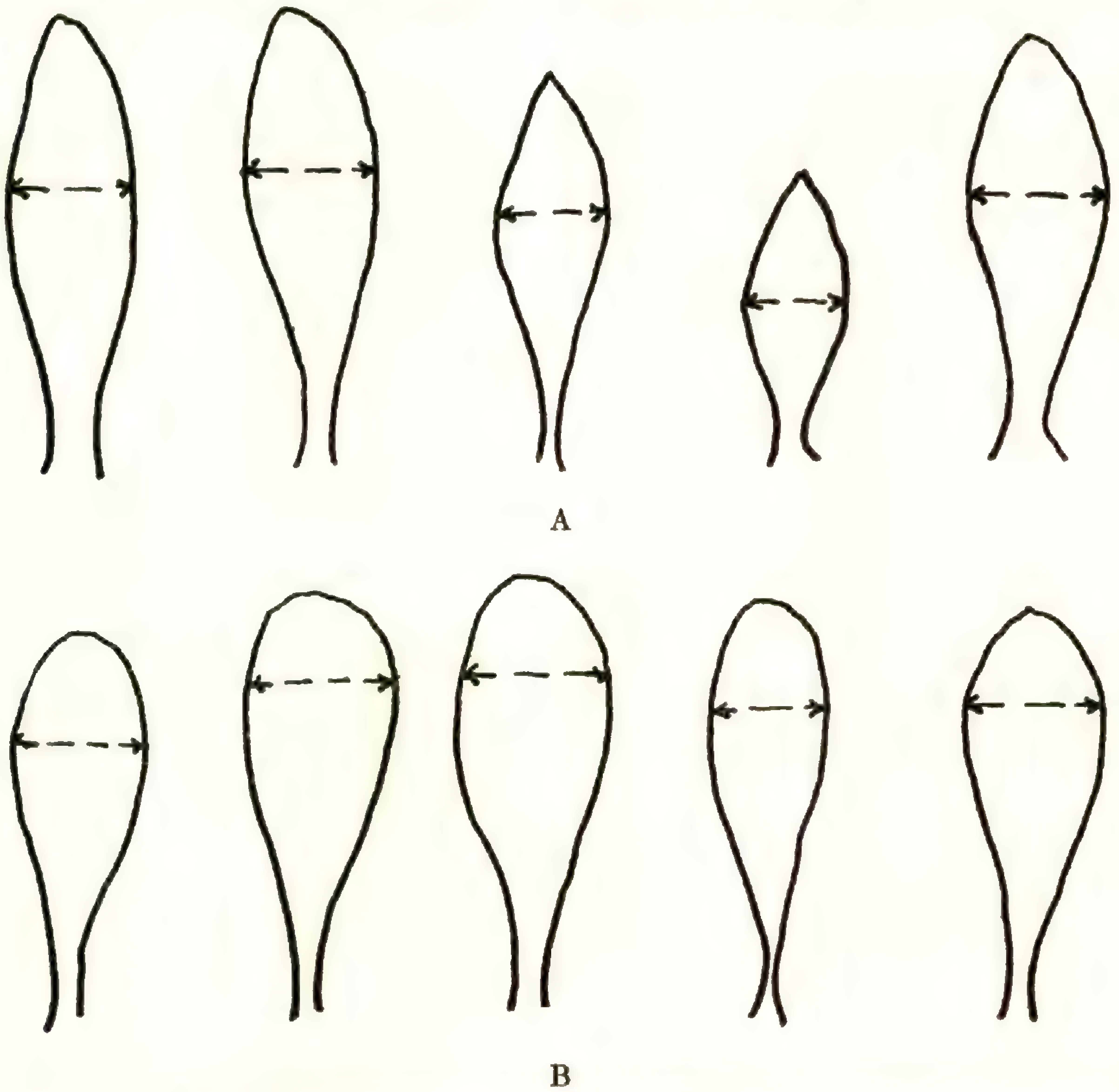


Fig. 6. *A*, outlines of five petals each of *I. versicolor; B*, outlines of five petals each of *I. virginica*,

of *Iris versicolor*. For the purpose of taxonomic description they may be conveniently and accurately separated by describing those of *Iris versicolor* as ovate-lanceolate and those of *Iris virginica* as

obovate-spatulate. To separate them by biometric methods is by no means so easy, as table v shows.

TABLE V

	Petal length	Petal width	Petal taper	Taper / width
	cm.	cm.	cm.	
Iris virginica				
No.				
1	4.2	1.4	1.5	1.1
2	4.7	1.7	0.8	0.5
3	4.8	1.7	0.9	0.6
4	4.6	1.3	1.1	0.9
5	4.6	1.6	1.2	0.8
Iris versicolor				
No.				
1	4.7	1.3	2.0	1.5
2	4.8	1.5	1.7	1.1
3	4.1	1.2	1.3	1.1
4	3.0	1.2	1.2	1.0
5	4.5	1.4	1.7	1.2

Neither the length nor the width will suffice. The taper (i. e. the length between the point of maximum width and the tip) is only somewhat better. The ratio between this latter measurement and the width is still better though it fails to separate the entire lot. None of the measurements is as good for purposes of distinction as the single terms "ovate-lanceolate" and "obovate-spatulate." Only by combining all three measurements into a complex ratio would it be possible to demonstrate, mathematically, the discontinuity between the two sets of petals. As Minot (quoted by Thompson, '17) has said, "The fact that men of genius have evolved wonderful methods of dealing with numerical relations should not blind us to another fact, namely, that the observational basis of mathematics is, psychologically speaking, very minute compared with the observational basis of even a single minor branch of biology. * * * While therefore here and there the mathematical methods may aid us, we need a kind and degree of accuracy of which mathematics is absolutely incapable."

The above example illustrates the two chief reasons why biometry must necessarily be limited in its application to taxonomy. In the first place, mathematics is swift and efficient only in recording differences in number; it becomes cumbersome in record-

ing differences in form, however useful it may be for a deeper analysis of the forces which produced the form. Yet it is just such differences in form which are most commonly met with in taxonomic work. This point is shown in a survey of the points on which specific distinction is based in two representative families. (one from the Monocotyledons and one from the Dicotyledons) in the seventh edition of Gray's 'Manual'. The differences were classified as being based on shape, on absolute size and number, and on comparative size and number. In all doubtful cases the preference was given to differences in number.

	Differences in shape	Differences in absolute size or number	Differences in comparative size and number
Iridaceae	21	13	12
Boraginaceae	31	11	9

There is an even more fundamental reason why the customary methods of mathematics are not well adapted to taxonomic work. Such methods are comparatively simple when the variations in one characteristic are being traced; they become involved and cumbersome when the simultaneous changes in a large number of variables are studied. Yet this last is essentially the method of the taxonomist. When he distinguishes between a group of sugar maples and a group of silver maples, for instance, he is summarizing a large number of differences—differences in form, size, color, and color pattern. Mathematics can deal with such problems through the study of correlation, but it is slow and laborious work and though it may be useful in the analysis of some particular problem it is not adapted to general taxonomic use.

An attempt has therefore been made to develop a new method of presenting biometric data which would combine the good points of the methods of mathematics and comparative morphology. Like mathematics, it is accurate and objective. Like morphology, it leaves something to the trained eye. This has been accomplished by diagramming the data in a series of ideographs. Figures 7 and 8 show how the four measurements on the petal and sepal are combined into a single figure. Essen-

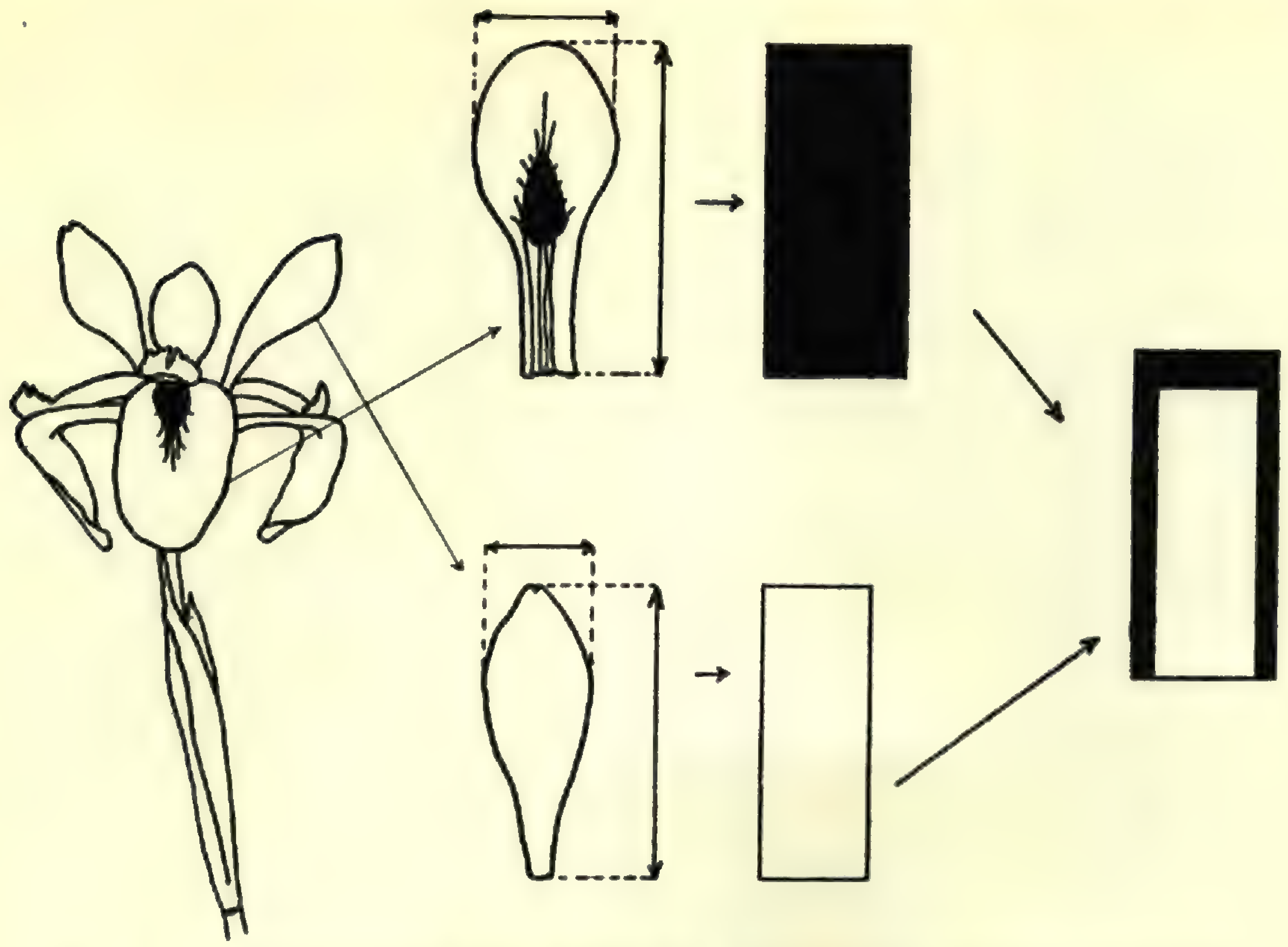


Fig. 7. Diagram showing typical flower of *I. virginica* and resulting ideograph.

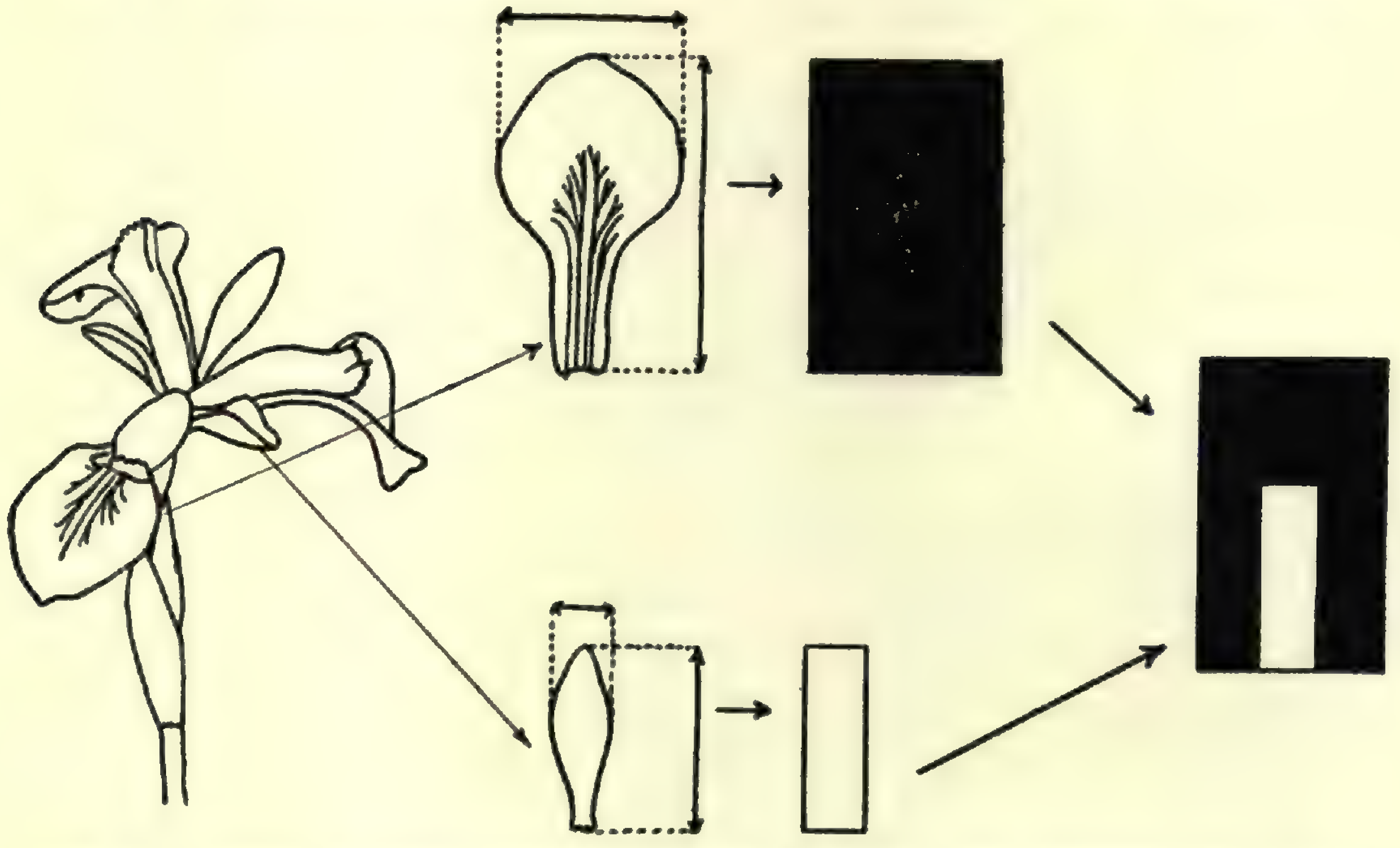


Fig. 8. Diagram showing typical flower of *I. versicolor* and resulting ideograph.

tially the ideograph consists of a diagrammatic white petal, superimposed upon a diagrammatic black sepal. By constructing an ideograph of this sort for each plant measured, it is possible

to show simultaneously the variation in the four variables considered, for an entire population of plants, or to compare the variation in one population with that in another as in figs. 10 to 13.

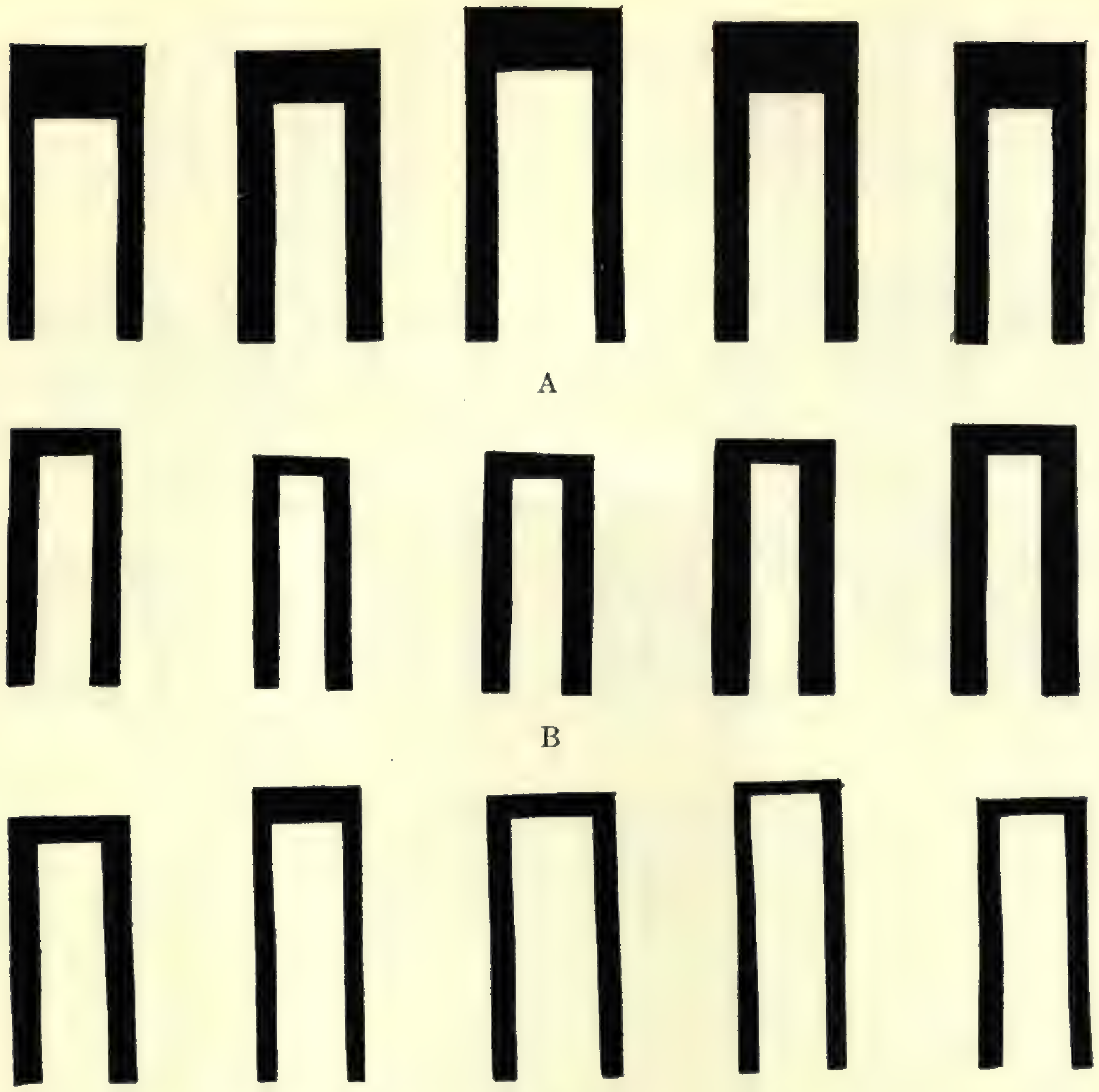
Such ideographs would seem to be of general usefulness in taxonomic work. They are capable of demonstrating slight differences in proportion which are not revealed by figures alone. In the genus *Iris*, for instance, though *Iris fulva*, *Iris foetidissima*, and *Iris prismatica* each belong to a different section of the genus, the three species have flowers of nearly the same size. The dimensions of the petals and sepals are so nearly the same that the species hardly appear distinct when the figures are compared, as in table VI. When these are arranged as ideographs, however, as in fig. 9, the essential differences in proportion between the three species are clearly demonstrated and they are seen to be morphologically distinct.

TABLE VI

COMPARISON OF FLORAL DIMENSIONS OF THREE SPECIES OF IRIS

	Sepal length in cm.	Sepal width in cm.	Petal length in cm.	Petal width in cm.
Iris prismatica	4.4 4.9 4.7 4.8 4.5	2.0 1.8 2.1 1.8 1.8	4.0 4.3 4.3 4.6 4.2	1.1 1.2 1.4 1.1 1.1
Iris fulva	4.9 4.9 5.6 5.3 5.0	2.2 2.4 2.6 2.4 2.2	3.7 4.0 4.5 4.1 3.9	1.4 1.2 1.6 1.3 1.1
Iris foetidissima	4.3 3.9 4.0 4.4 4.5	1.8 1.6 1.8 2.0 2.1	3.9 3.6 3.6 3.9 4.0	0.9 0.8 0.9 0.8 0.9

Ideographs for twenty individuals each of sixteen representative colonies are grouped in figs. 10–12 (*I. virginica*) and fig. 13 (*I. versicolor*). They give another proof of the striking variation in size and proportion which has been found in every colony studied. In marked contrast to the variation between individuals is the general resemblance between colonies of the same species. While several different colonies have slight



A

B

C

Fig. 9. *A*, ideographs of five plants of *I. fulva; B*, ideographs of five plants of *I. foetidissima; C*, ideographs of five plants of *I. prismatica.*

individual tendencies, and while in the case of those colonies which have been measured in successive years (fig. 10) the peculiarities persist from year to year, there is practically no differentiation between one region and another. The only generalization that can be made is that *Iris versicolor* becomes on the average a little smaller as one goes from north to south and that *Iris virginica* becomes a little larger. Thus, although the colony at Stanton, Kentucky (fig. 12), seems slightly unusual by reason of its comparatively large petals the other colonies studied in Kentucky and Tennessee (Bonnieville and Camden) do not show these peculiarities. There is as much variation in proportion and almost as

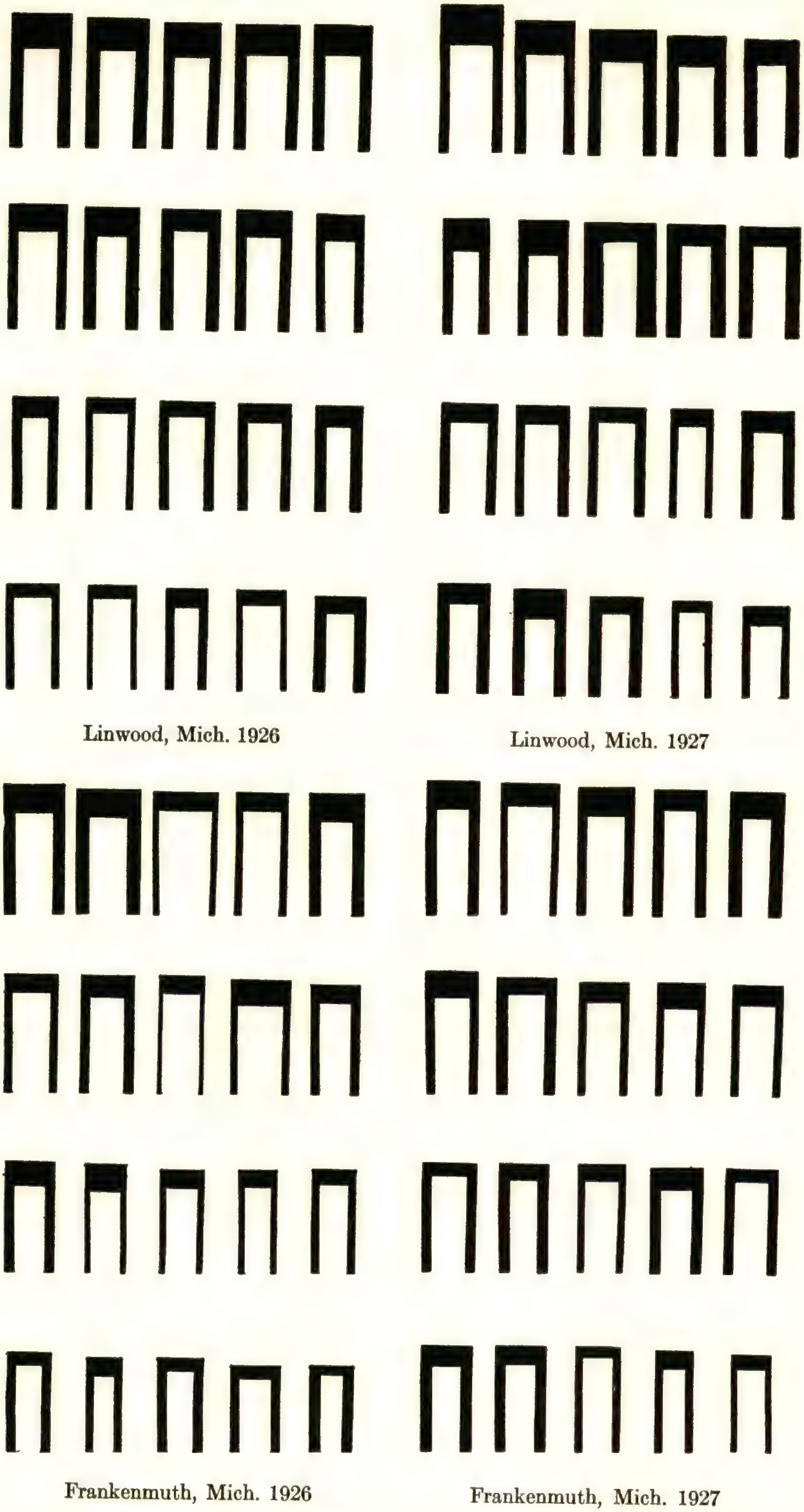


Fig. 10. Ideographs of twenty individuals each of four colonies of *I. virginica*.

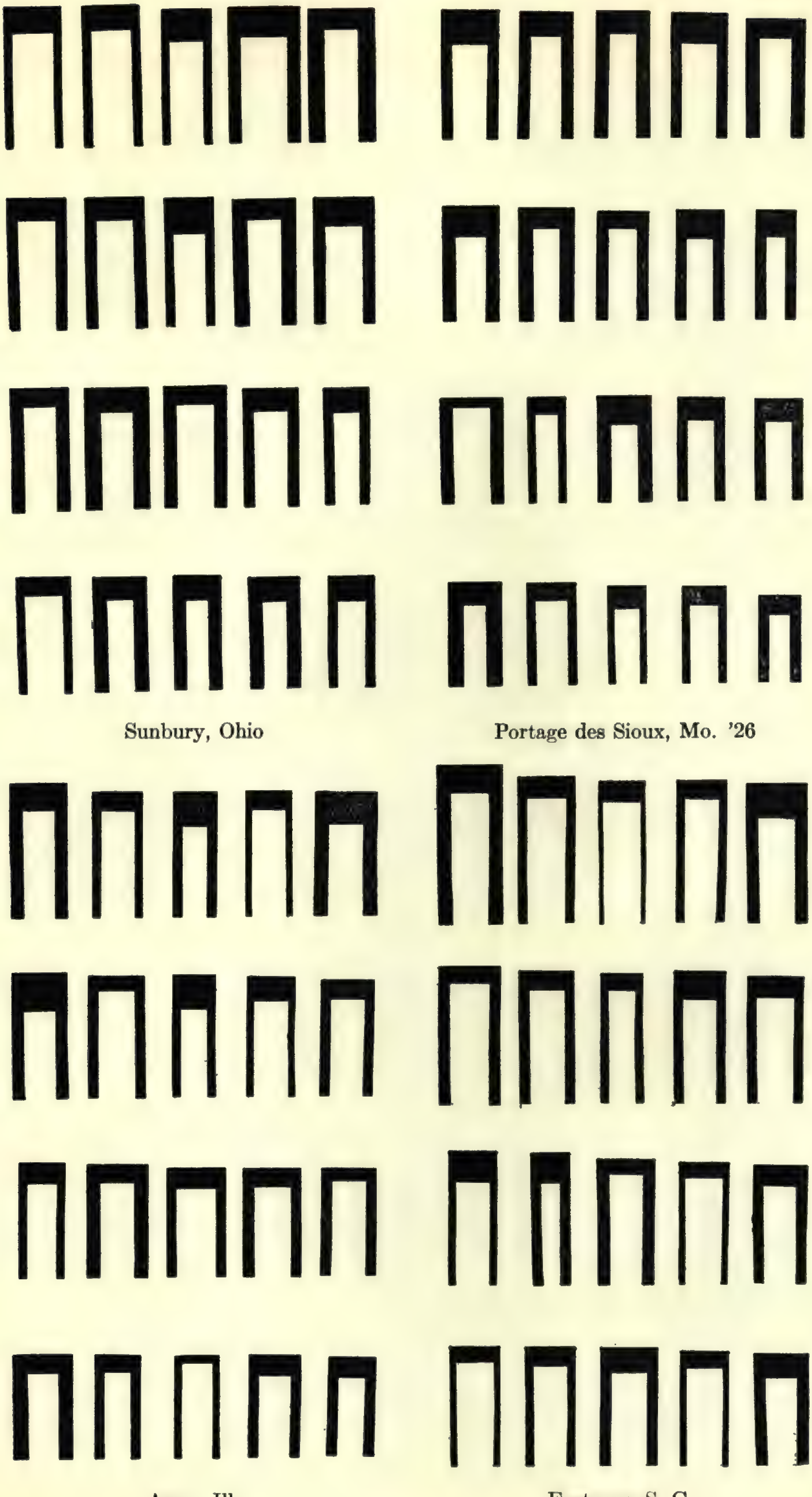


Fig. 11. Ideographs of twenty individuals each of four colonies of *I. virginica*.

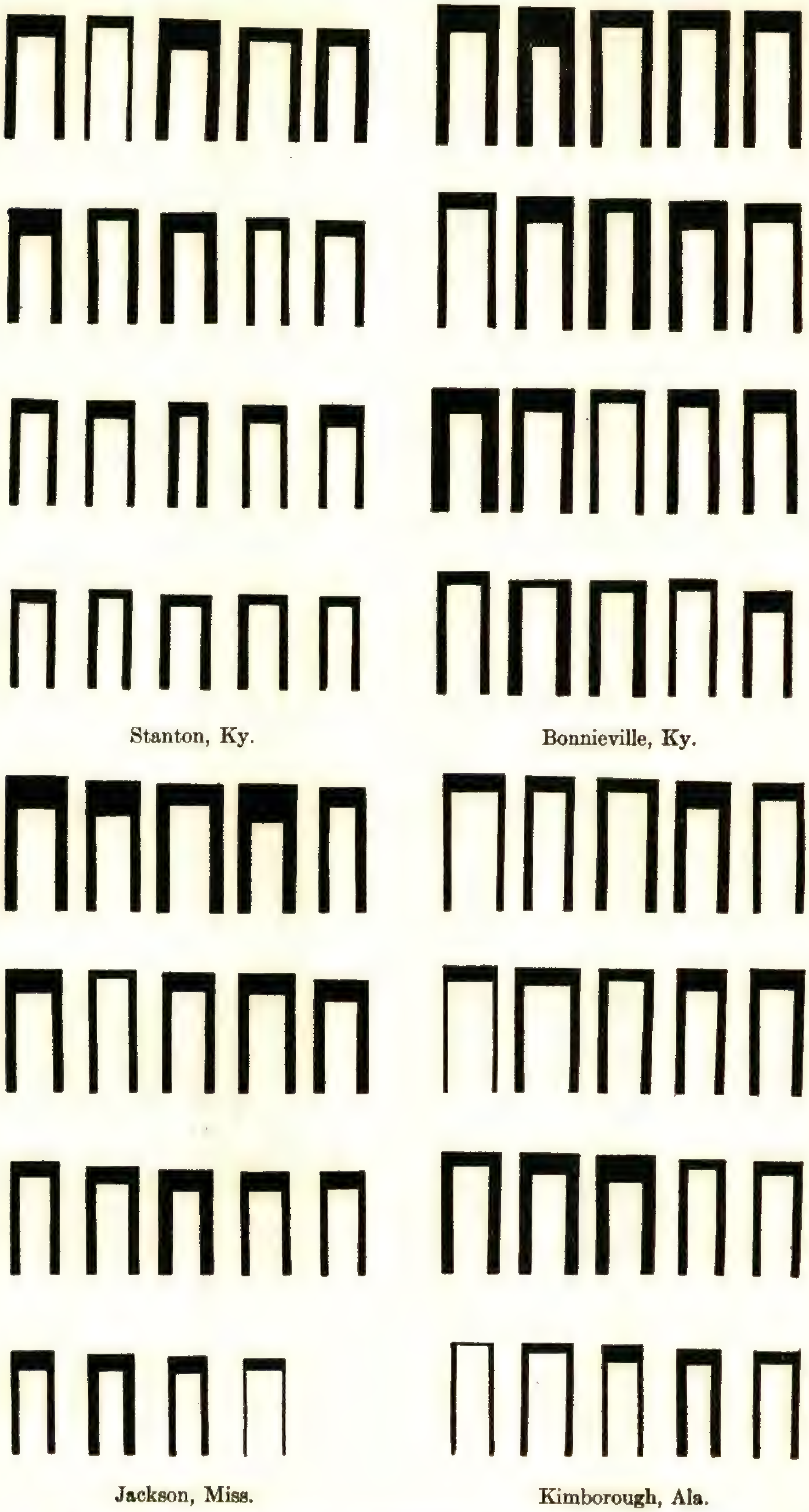


Fig. 12. Ideographs of twenty individuals each of four colonies of *I. virginica*.

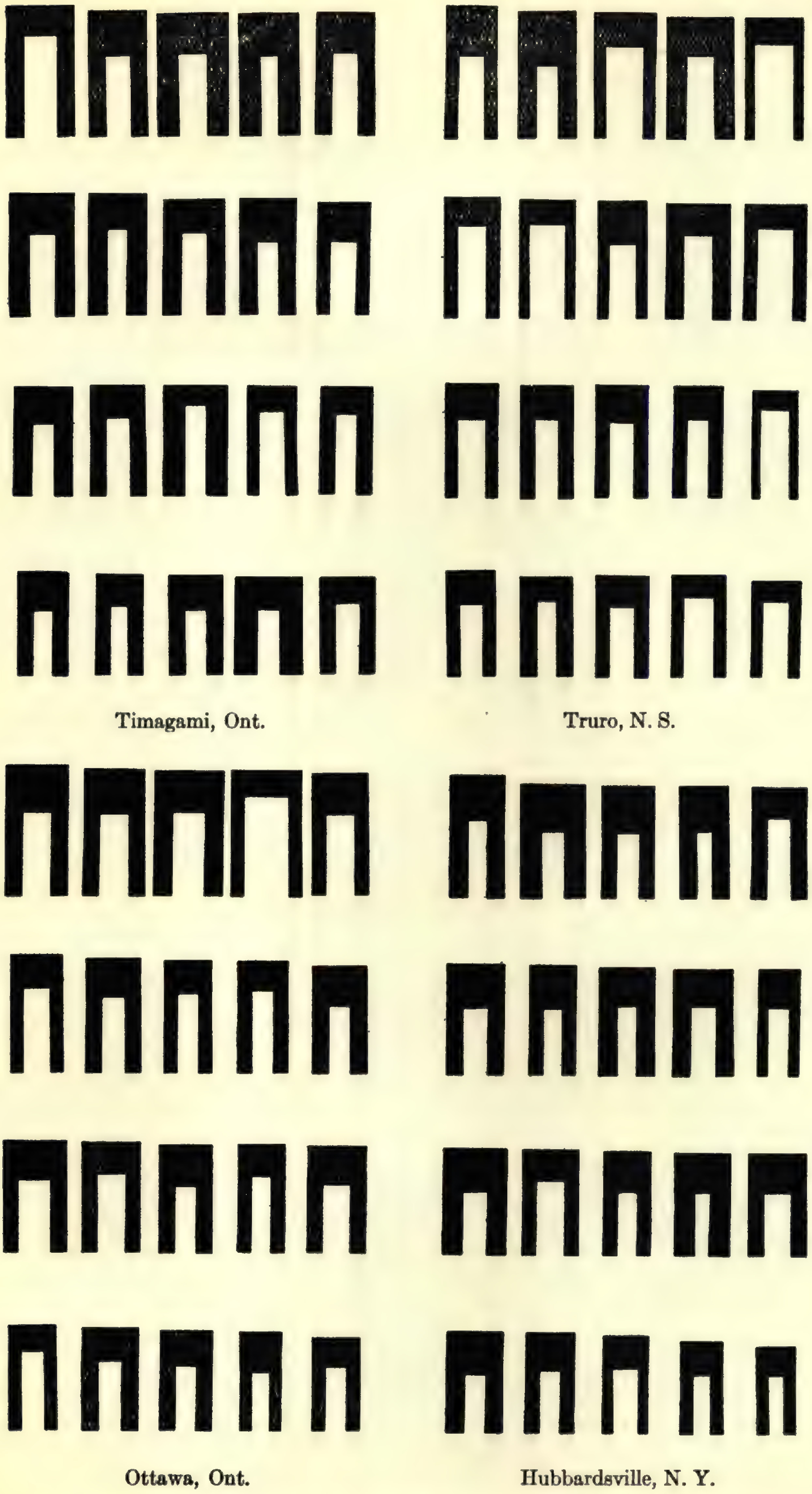


Fig. 13. Ideographs of twenty individuals each of four colonies of *I. versicolor*.

much in size in the colonies from southern Michigan as there is within the whole group of colonies of *Iris virginica* from the Great Lakes to the Gulf of Mexico.

Above all, when the ideographs are considered as a whole, the two species remain completely and absolutely distinct. In spite of a wide range of variation in separate characteristics, when the combination as a whole is studied it is found to be strikingly

TABLE VII

MEDIAN MEASUREMENTS OF IRIS FLOWERS FROM DIFFERENT LOCALITIES

IRIS VIRGINICA

Number of individuals	Locality	Year	Median sepal length in cm.	Median sepal width in cm.	Median petal length in cm.	Median petal width in cm.
25	Kimborough, Ala.	1927	6.3	2.8	5.7	1.8
21	Jackson, Miss.	1927	5.9	2.6	4.9	1.8
50	Camden, Tenn.	1926	6.7	3.0	5.7	2.0
35	Bonnieville, Ky.	1926	6.7	3.0	5.7	1.8
21	Stanton, Ky.	1926	5.5	2.6	4.9	1.6
20	Eastover, S. C.	1928	6.7	2.8	5.7	1.9
15	Maysville, N. C.	1928	7.5	3.0	6.1	2.0
38	Anna, Ill.	1926	6.3	2.8	4.9	1.8
27	Vulcan, Ill.	1925	6.3	2.6	5.3	1.8
15	Vulcan, Ill.	1926	6.3	2.6	5.3	1.6
38	Farmington, Ark.	1925	6.3	3.0	5.3	2.2
43	Wicks, Mo.	1925	5.9	2.6	4.5	1.6
23	Valley Park, Mo.	1926	5.9	2.8	5.3	1.8
40	Portage des Sioux, Mo.	1926	5.9	2.8	4.9	1.6
30	Portage des Sioux, Mo.	1927	6.3	3.0	5.7	2.0
28	Portage des Sioux, Mo.	1928	6.8	3.2	5.8	2.0
27	Louisiana, Mo.	1924	6.3	2.8	5.3	1.6
26	Fort Madison, Ia.	1924	5.9	2.8	4.5	1.6
30	Sunbury, O.	1927	6.7	3.0	5.3	1.9
28	Mill Creek, O.	1925	5.1	2.1	4.1	1.4
23	Huron, O.	1925	5.5	2.4	4.1	1.4
63	Bay Bridge, O.	1925	5.1	2.4	4.1	1.4
33	Middle Bass Is., O.	1925	5.1	2.6	4.5	1.6
30	Lawrence, Mich.	1926	5.9	2.8	4.9	2.0
30	Schoolcraft, Mich.	1926	5.9	2.6	4.9	1.8
30	Centerville, Mich.	1926	6.3	2.8	5.3	1.8
35	Hartland, Mich.	1926	5.9	2.8	4.9	1.8
25	Armada, Mich.	1924	5.5	2.2	4.1	1.4
45	Yale, Mich.	1924	5.5	2.4	4.5	1.7
43	Otisville, Mich.	1924	5.5	2.4	4.5	1.6
19	Otisville, Mich.	1926	5.5	2.4	4.5	1.8
35	Frankenmuth, Mich.	1926	5.9	2.6	4.9	1.8
30	Frankenmuth, Mich.	1927	5.9	2.8	4.9	1.8
30	Linwood, Mich.	1926	5.9	2.9	4.9	2.0
25	Linwood, Mich.	1927	5.9	3.0	4.9	1.8
25	Muskegon, Mich.	1924	5.5	2.4	4.5	1.6
52	La Crosse, Wis.	1924	5.9	2.6	4.9	1.6
27	Pardeeville, Wis.	1927	5.5	2.8	4.9	1.8
33	Slinger, Wis.	1924	5.9	2.4	4.9	1.8

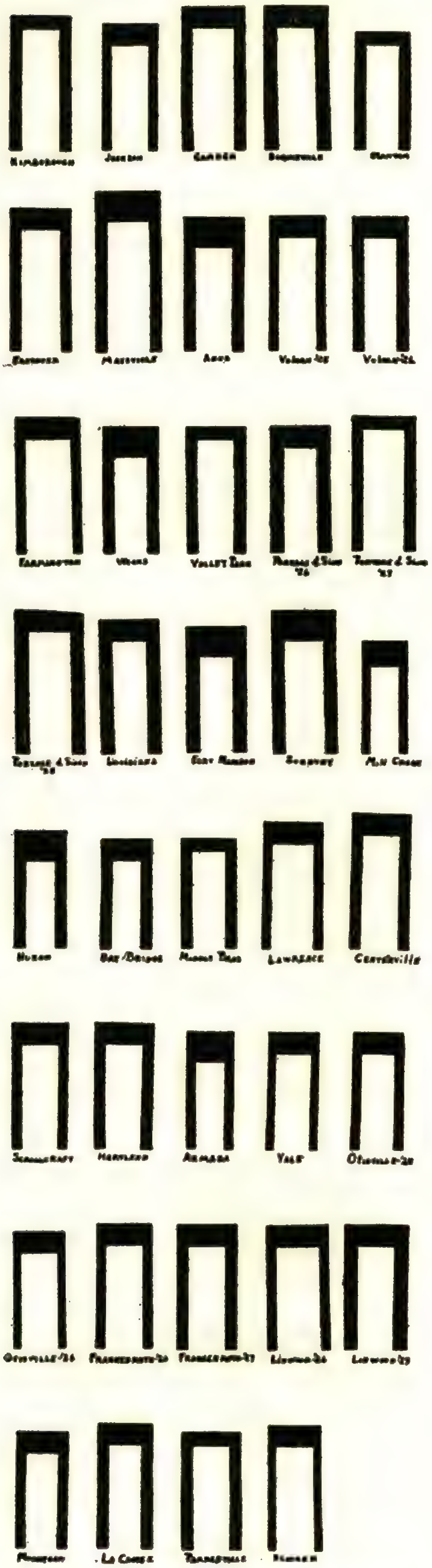
IRIS VERSICOLOR

Number of individuals	Locality	Year	Median sepal length in cm.	Median sepal width in cm.	Median petal length in cm.	Median petal width in cm.
28	Hood, Md.	1927	5.9	2.8	3.7	1.2
22	Liverpool, Pa.	1927	5.9	3.0	4.1	1.4
35	Harmonsburg, Pa.	1925	5.5	2.8	3.3	1.2
29	Conewango, N. Y.	1924	5.9	3.2	4.1	1.8
28	Villenova, N. Y.	1927	5.9	3.0	4.1	1.6
35	Hubbardsville, N. Y.	1925	5.5	2.6	3.3	1.0
27	Pownal, Vt.	1925	5.1	2.2	3.3	1.0
38	Pownal Center, Vt.	1925	5.1	2.4	3.3	1.1
37	Clarendon, Vt.	1925	5.1	2.6	3.3	1.0
34	New Haven Jct., Vt.	1926	5.9	3.0	4.1	1.5
25	Middlebury, Vt.	1926	5.9	3.0	4.1	1.4
20	Duxbury, Mass.	1927	5.5	2.8	3.7	1.4
26	Alberton, Ont.	1927	5.5	3.0	4.1	1.6
32	Ottawa, Ont.	1926	5.9	3.0	4.1	1.4
26	Timagami, Ont.	1926	5.9	3.2	4.1	1.2
22	Truro, N. S.	1927	6.3	2.8	4.1	1.4

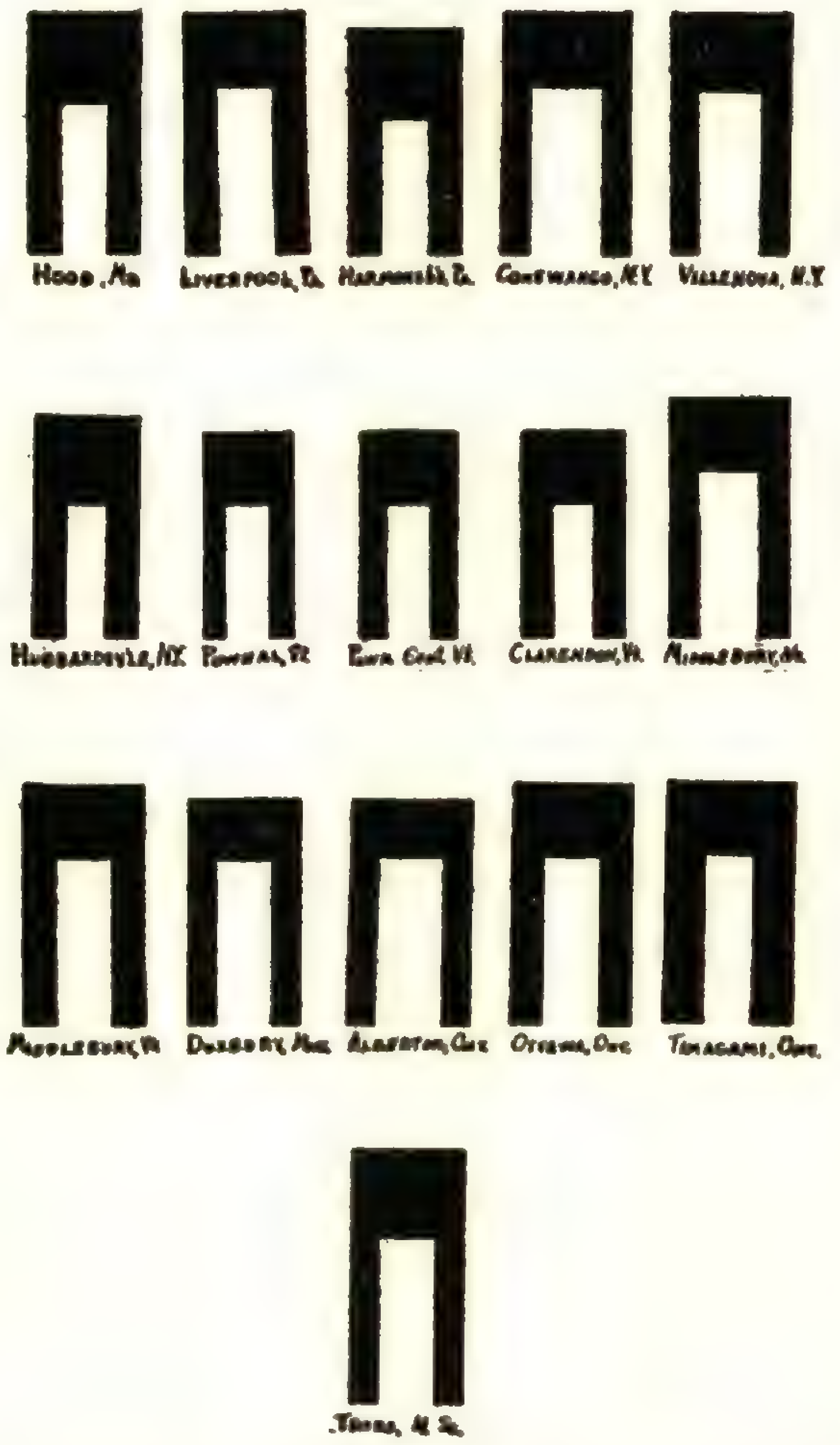
constant. *Iris versicolor* remains always and unmistakably *Iris versicolor.* and *Iris virginica* remains always and unmistakably *Iris virginica.* There is not the slightest tendency for one species to merge into the other.

By employing another mathematical concept, that of the average, we can construct a different sort of ideograph and produce something like a composite picture of each colony. If for each colony we take the average length of sepal, average width of sepal, average length of petal, and average width of petal, and construct an ideograph we will obtain a figure which will present graphically the averages of all four measurements for the colony in question. It will be a purely hypothetical figure; it will not necessarily present the kind of proportions most commonly met with in the particular colony but it will serve for convenient comparison between separate colonies and between successive measurements of the same colony. As in the earlier presentation of averages, the median is used rather than the mathematical mean because it is less influenced by occasional extreme values. The median values and also the number of individuals measured are presented in table VII. The resulting ideographs are shown in fig. 14.

The examination of these composite ideographs strengthens the conclusions already arrived at. The differences between colonies



Composite ideographs of 39 colonies of *I. virginica.*



Composite ideographs of 16 colonies of *I. versicolor.*

Fig. 14.

are very slight. In spite of the fact that the colonies measured extend from the Gulf Coast to the Great Lakes in the case of *Iris virginica,* and from Maryland to the north woods in the case of *Iris versicolor,* there is practically no evidence of regional differentiation; that is, of the formation of morphologically distinct geographical subspecies within either *Iris versicolor* or *Iris virginica.* As before, *Iris versicolor* is seen to become slightly dwarfed towards the South, whereas *Iris virginica* is smaller in the North. The general proportions of each species, however, remain strikingly similar throughout their entire ranges. There is no outstanding difference in proportion which characterizes any one region, though individual colonies may show slight peculiarities. Thus while the colony at Wicks, Missouri, is distinctive by reason of its proportionately small petals, that at Valley Park, Missouri, only a few miles away, is characterized by proportionately large ones, while the near-by colonies of Portage des Sioux, Missouri, and Vulcan, Illinois, have petals of about average proportions.

In addition to differences in size and proportion, another sort of difference has been noted in the plants grown in the experimental garden. There is a general tendency, in both species, for the plants from northern colonies to come into bloom sooner than those from southern colonies. There is a good deal of variation in blooming time within each locality, of course, and this will mask the general tendency to a certain extent but for three springs it has been observed that the earliest plants to come into bloom are from northern colonies and the latest are those from southern ones.

Aside from differences in size and in blooming periods no consistent regional differences have been found within either species. It is, of course, possible that such differences existed but were not revealed by the methods used. However, these methods did distinguish successfully between the two species. If regional differences do exist, they must be of an entirely different order of value from the differences between species.

CHARACTERISTIC TENDENCIES

Quite as remarkable as any clear-cut differences between the two species were certain characteristic tendencies of one or the

other species to depart from the normal. The spathe valves of the two species are usually very similar, the longest ones of *Iris versicolor* and the shortest of *Iris virginica* being quite indistin-

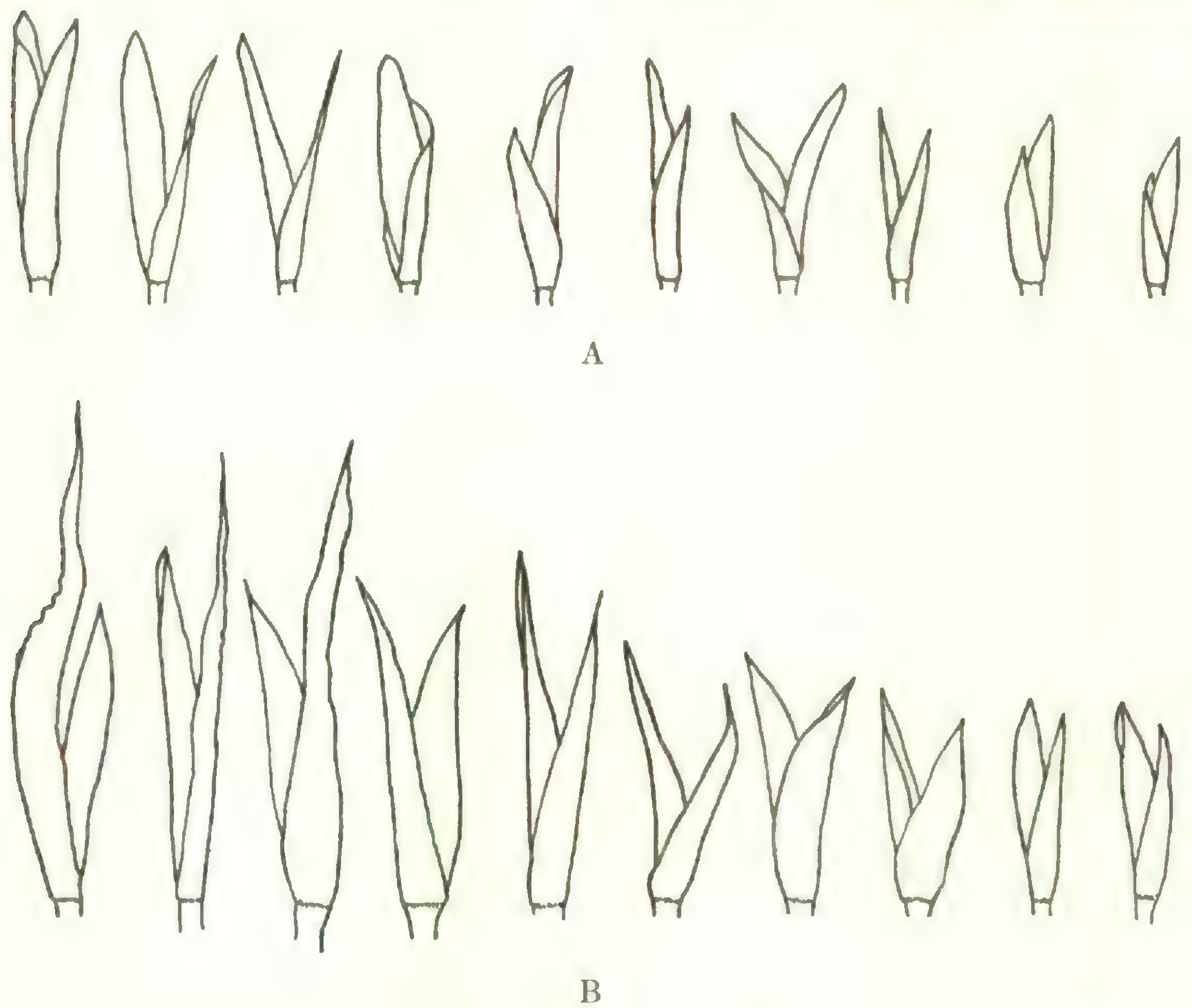


Fig. 15. *A*, range of variation in spathe valves of *I. versicolor*, × ½; *B*, range of variation in spathe valves of *I. virginica*, × ½.

guishable morphologically. Those of *Iris virginica*, however, occasionally become long and foliaceous like those of *Iris hexagona;* those of *Iris versicolor* were never seen to do so. *Iris virginica* often (in nearly 50 per cent of the cases examined) had a terminal notch in the petal. Only twice have such notches been seen in *I. versicolor.* They were not due to mutilation, since they could be found in buds several days before opening; they were probably correlated with a dichotomy of the vascular system of the petal. More or less associated was a tendency on the part of *Iris virginica* to produce ruffled, crimped, or even crenate petals. Flowers exhibiting these characteristics are shown in pl. 34. Only once or twice was the tendency observed in *Iris versicolor* and even

then it was not highly developed. These are only a few of a host of variable characters which were occasionally expressed in one species and rarely or never in the other.

There is nothing new in this experience. It has been the common lot of all who have attempted to distinguish groups of organisms, be they species or families or phyla. The quotation from Bergson which Mrs. Arber ('25) uses in distinguishing between the Monocotyledons and the Dicotyledons is quite as appropriately used here as there. "The group must not be defined by the possession of certain characters but by its tendency to emphasize them."

The point in calling attention to this commonplace phenomenon is to suggest that if most of the differences between species are of this sort, taxonomists might well undertake surveys of variation within the species they are treating, on a scale much larger than is customary at the present time. Such studies should be particularly important in any attempt at a phylogenetic treatment of related species. *Iris virginica* is closely related to *Iris hexagona,* for instance, and one of the morphological indications of this relationship is that in about one case out of fifteen or twenty the spathe valves of *Iris virginica* are foliaceous like those of *I. hexagona.*

PECULIAR FORMS

A few of the individuals observed have been so unusual as to deserve special mention.

Albinos.—Complete albinos with no trace of color other than yellow have been found only in *I. virginica.* These were found at two places, at Lawrence, in western Michigan, and near Lake Saint Clair, in Ontario. Partial albinos are fairly common in both species. They are white, shaded or faintly lined with blue. They have been observed at the following localities:

I. virginica—Lawrence, Michigan (in same colony with albino); Farmington, Arkansas; Maysville, S. C.; Dennison, Mich.

I. versicolor—Timagami, Ontario; Central Connecticut (M. E. Mains).

Occasional individuals were found in each species in which the flower color is lavender or red-purple instead of blue. One such

form has been offered in flower catalogues for some years under the name of *I. versicolor kermisina.* Similar color forms have been found at the following localities:

I. virginica—Otisville, Mich.; Burke, Iowa; Camden, Tenn.
I. versicolor—Stratford, N. H.; Hubbardsville, N. Y.

Occasional individuals were found with sepals strongly reflexed. Three flowers from such an individual are illustrated in pl. 39, figs. 7–9.

THE GENETIC RELATIONSHIPS OF INDIVIDUAL DIFFERENCES IN IRIS VERSICOLOR

An experiment is under way to determine, for each species, the extent to which the peculiarities which characterize individual plants are passed on to their offspring, under the conditions obtaining in nature; in other words, to determine, from an inspection of the variation between sister seedlings, the amount of interbreeding which takes place under natural conditions. If the species is naturally self-fertilized ninety-nine times out of a hundred, all seedlings grown from a single parent plant should be practically alike and similar to the parent. If, however, there has been continuous out-crossing with other individuals, the sister seedlings should differ from each other and from the parents; as much, for instance, as human brothers and sisters differ from each other.

Several such series of sister seedlings from seed-pods collected on plants of *Iris versicolor* at Connecticut Lakes, N. H., bloomed in 1928. There were not enough flowers per plant to make careful qualitative studies but there were sufficient to allow certain preliminary conclusions to be drawn. One of these series is illustrated in pl. 40, and shows one flower from each of five sister plants. It will be noted that while the flowers are in general very similar, they are not as much alike as flowers from the same plant (see pls. 37, 38 and 39, where series of flowers from the same plants are illustrated). They are, however, much more alike than are the general run of individuals in a colony (see pl. 34).

The most conspicuous differences are in regard to the petals. Those of figs. 9, 5, and 6 (pl. 40) are unusually broad and flat, those

of number 7 are somewhat smaller, while number 8's are narrow and folded. There were accompanying differences in color which are only suggested by the photographs. Number 8, for instance, was distinctly lilac, while the others were blue. Similar results have been obtained in all the series of *Iris versicolor* which have blossomed to date. It is therefore concluded that *I. versicolor*, though usually self-fertilized, is frequently cross-pollinated under natural conditions. The relation of this conclusion to the question of Jordanons or micro-species, is deferred to the Discussion.

Hybridization of Iris versicolor and Iris virginica

A preliminary report

It has been found upon experiment that *Iris versicolor* and *Iris virginica* are partially fertile in crosses with each other. There has not yet been enough material in the breeding plot to make exact quantitative studies, but whereas nearly all the crosses which have been tried *within* either species have set seed, only

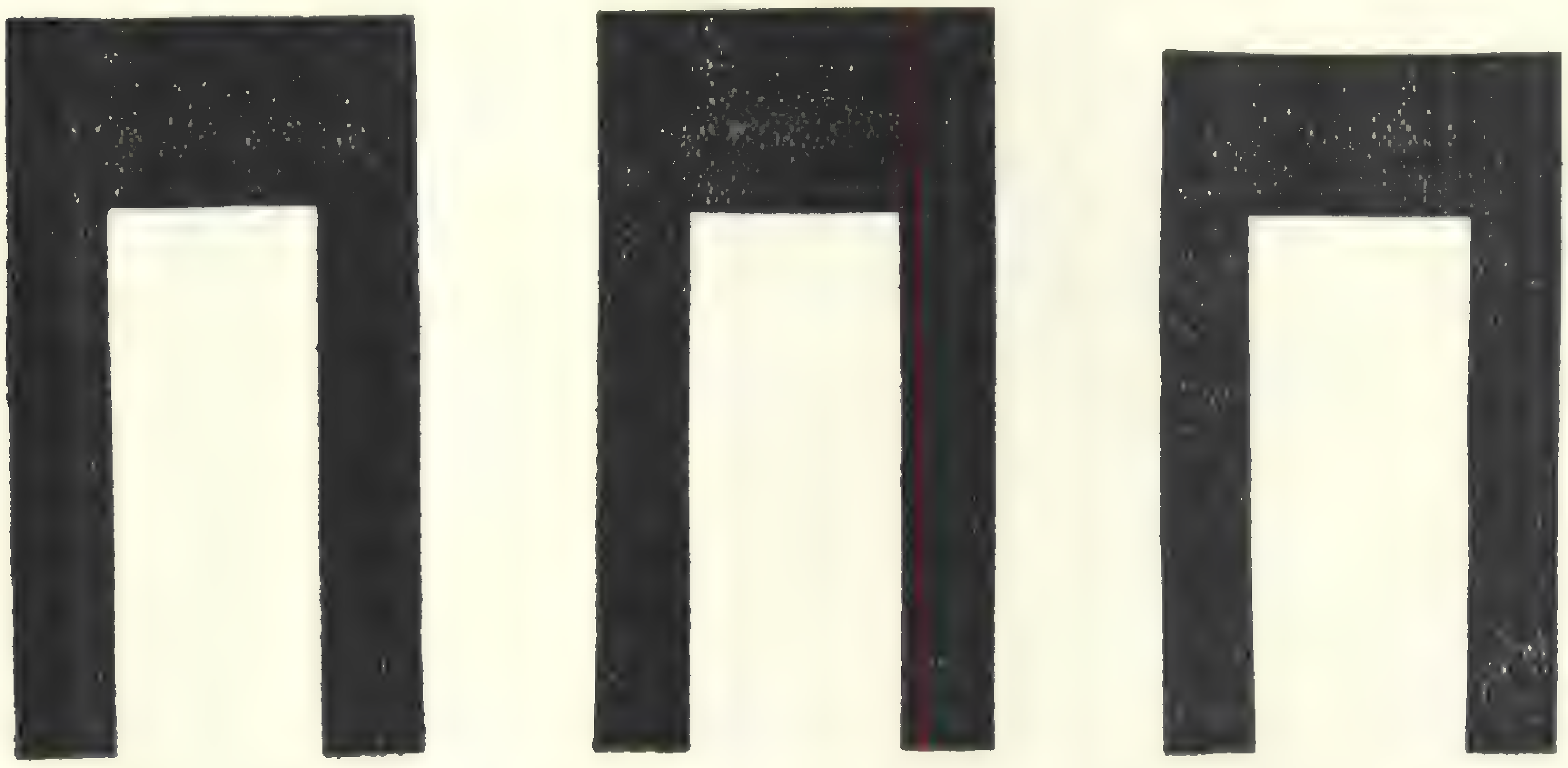


Fig. 16. Ideographs of three hybrid plants; left, natural hybrid from Engadine, Mich.; center, artificial hybrid produced at the Missouri Botanical Garden; right, natural hybrid from London, Ontario.

slightly more than half of those *between* the two species have done so. The resulting hybrid seed has a low percentage of germination and the seedlings show hybrid vigor. This was particularly noticeable when the young seedlings were grown in the cold-frame side by side with seedlings of the parent species. The seedlings

of *Iris versicolor* and of *Iris virginica* varied greatly in vigor, whereas the hybrid seedlings were all uniformly vigorous.

Of the various crosses which have been made, two have flowered. They are reciprocal crosses between plants I-AAA-3 and IAAG. I-AAA-3 is a plant of *Iris virginica* collected at Flint, Michigan, in 1923, and is illustrated in pl. 41, right figures. It is large-flowered and the flower has bright blue veining on a light background. The petals are unusually broad. IAAG is a plant received from Dr. J. R. McLeland of Pleasanton, Kansas, though it came originally from Medina, N. Y. It is a typical *Iris versicolor* and is outstanding in the dark color of its flowers and its stems. It is illustrated in pl. 41, left figures.

The seedlings of cross IXB (I-AAA-3 × IAAG) were similar in size, leaf number, leaf height, etc., to the most vigorous plants of either parent species. The seedlings of the reciprocal cross, IXA (IAAG × I-AAA-3) were even more vigorous. Plants one and two years old grown from seed showed leaves one fourth again as high and about half again as many leaves per plant as the parents.

IXA and IXB flowered for the first time in 1927. Ideographs and photographs of their flowers and of those of the parent species are shown in fig. 16 and pl. 41. It should be emphasized that the measurements and pictures of IXA and IXB were made from plants growing in the cold-frame. They would have been much larger if grown in the water-side plots with the other plants. Thirteen plants of IXA and three plants of IXB were brought to flowering age. The two sets of hybrids were very similar aside from the greater vigor of IXA. While the seedlings varied slightly among themselves they were remarkably uniform in general aspect. They were intermediate in all the differences which characterize the two parents, though they were easily distinguished by their vegetative vigor. In general appearance and in practically all measurable characters they much more closely resembled *Iris versicolor* than *Iris virginica*. Their most outstanding differences from *Iris versicolor* were their much larger and laxer petals and the peculiar spots at the base of the sepal. The spots were due to the combination of the bright yellow pubescent spot of *Iris virginica* and the dark blue cross-

veining and brown stippling of *Iris versicolor*. The resulting "eye" is unlike anything in either species.

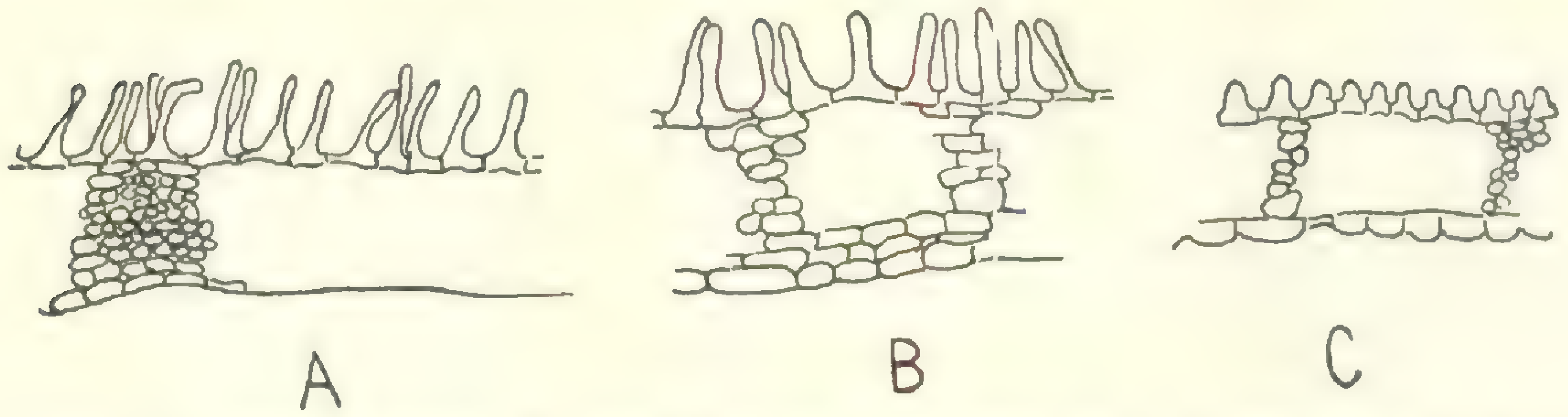


Fig. 17. Cross-sections of sepals showing pubescence: *A*, *I. virginica; B, I.* × *robusta; C, I. versicolor;* × 25.

A microscopical examination of the pubescence of the sepal showed that of the hybrid to be intermediate in form between the two species though, due to the larger cells of the hybrid, it is almost as long as that of *Iris virginica*. Camera-lucida drawings of all three are shown in fig. 17. The hybrid was likewise intermediate in the glandular development at the base of the stamens. Figure 18 shows cross-sections of the perianth tubes.

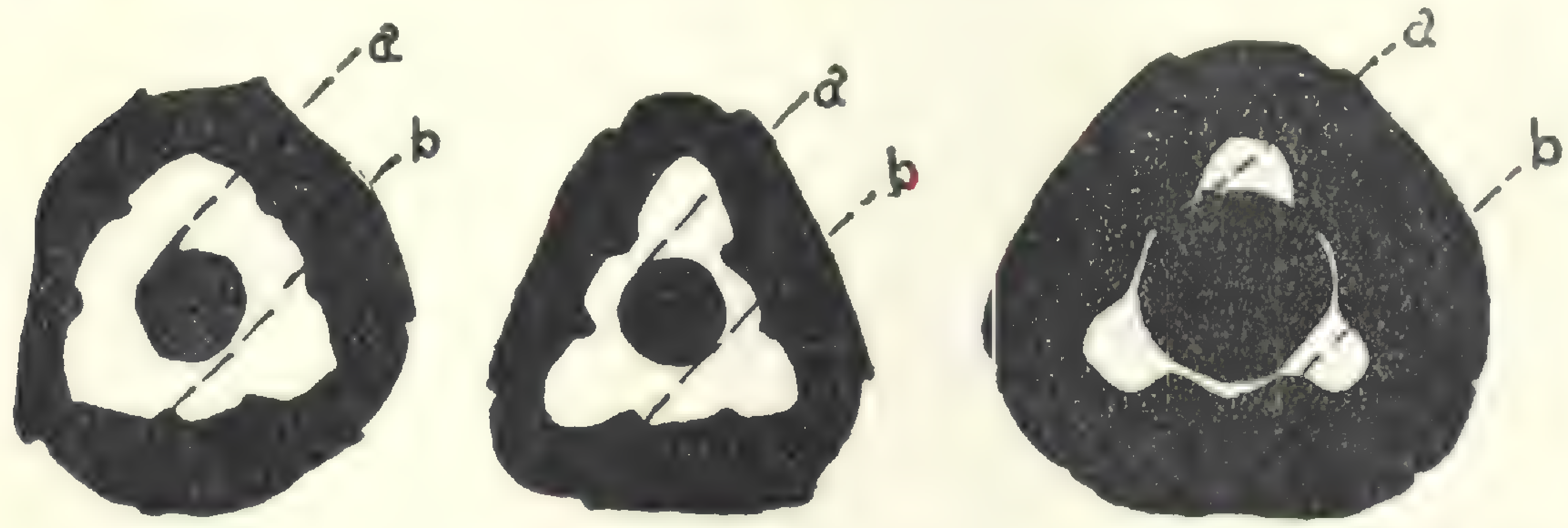


Fig. 18. Cross-sections of perianth tubes showing, *a*, style, and *b*, glandular development of inner wall of tube; left, *Iris versicolor*, right, *I. virginica*, center, *I.* × *robusta*.

The plants of crosses IXA and IXB were partially sterile. Counts showed about 50 per cent abnormal pollen and many of the ovules aborted. Ovaries with one exposed locule are shown in pl. 41. The plants from which the capsules were taken were growing in the same cold-frame and had had an equal opportunity for pollination. All of the seed capsules on the hybrid plants were small and shrunken.

Numerous other hybrids between the two species have been

made, and while they have not flowered they are similar in their vegetative characteristics to those already described. Dr. J. R. McCleland, an iris amateur of Pleasanton, Kansas, has grown several crosses between the two species, some of which I have seen, and they are similar to IXB and IXA.

Natural hybrids resembling those produced in the experimental plot have been found at several points where the ranges of the two species overlap. They would be commoner were it not for the barriers which exist between the two species; geographical barriers such as the extensive limestone areas west of the Alleghenies in which neither species is common; physiological barriers which prevent them from being wholly fertile with each other. The location of the hybrids and their relation to the distribution of the parent species is shown in fig. 19.

Most of the hybrids found were very similar to those produced in the experimental plot. Those observed in Ontario resembled the garden-made hybrids very closely. There was little variation between them although they were found in several places. They were nowhere particularly abundant except in one creek bed just west of London, Ontario, where there was a large colony, apparently all belonging to one clone. *Iris virginica* was fairly common throughout this district. *Iris versicolor* was not found there though it was fairly common a short distance east of London.

At Yale, Michigan, a single plant of *Iris versicolor* and a few hybrids were found. They were in a meadow near a small graveyard from which *I. versicolor* may have spread. There were no plants of *Iris virginica* in the immediate neighborhood, though it is common in eastern Michigan and there were large colonies within two miles. An extensive search of the neighborhood failed to locate any other plants of *Iris versicolor* or of the hybrids.

At Tawas City, Michigan, a single hybrid plant was found growing along the roadside among a group of plants of *Iris versicolor*. A colony of *Iris virginica* was found less than half a mile away.

At only two points were the hybrids found making up large colonies. These were both in the northern peninsula of Michigan, and though only a few miles apart they were so different in their composition that a separate description will be given of each.

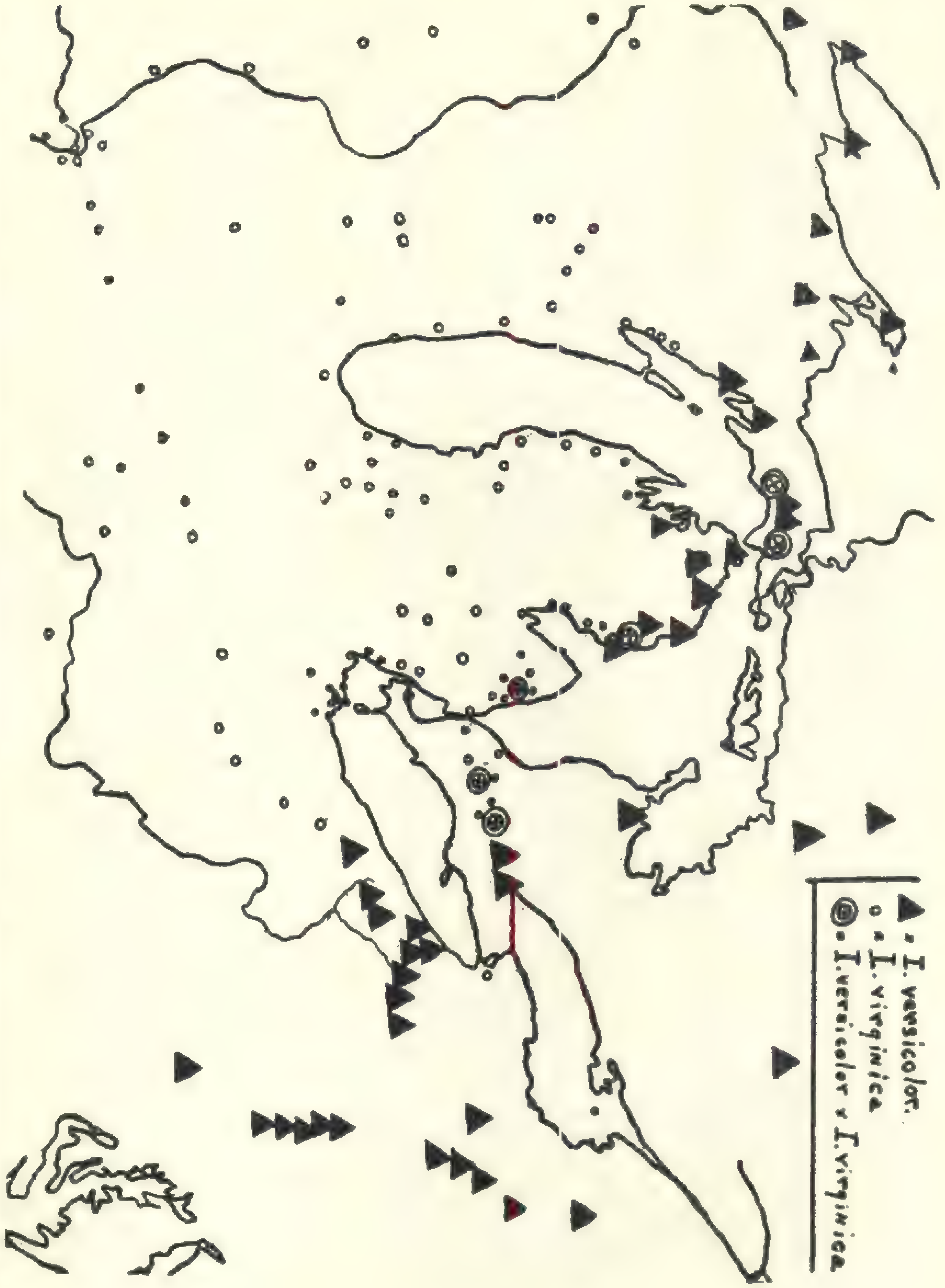


Fig. 19. Distribution of natural hybrids between *I. versicolor* and *I. virginica* (*I.* × *robusta*) in relation to that of the parent species.

WEST ST. IGNACE

Along the main highway three miles west of Saint Ignace a very remarkable colony was located. It had apparently originated by the intermingling of the two species, followed by numerous crosses and back crosses. The ideographs in fig. 20 give a slight idea of the bizarre mixture of types which was encountered; there was everything from typical *versicolor* to typical *virginica* with numerous intermediates and a number of very curious forms unlike anything seen before either in wild colonies or in the experimental plot. Most of the plants exhibited a high degree of vegetative vigor, though the environment did not seem to be unusually favorable.

ENGADINE

At Engadine, a few miles west of West St. Ignace another peculiar colony was found. It was most remarkable by reason of the great vegetative vigor of the plants. There was a degree of variation between the plants quite comparable to that found in colonies of the parent species, but by no means so extreme as that found in the colony at West St. Ignace. The plants were all very similar in their general aspect to the hybrids produced in the experimental plot. Ideographs of the colony show its lesser variability, and show the general similarity to the experimentally produced hybrid in fig. 16.

Though admittedly difficult, if not impossible, to distinguish by means of ordinary herbarium material, the hybrid appears of sufficiently common occurrence to warrant a special name.

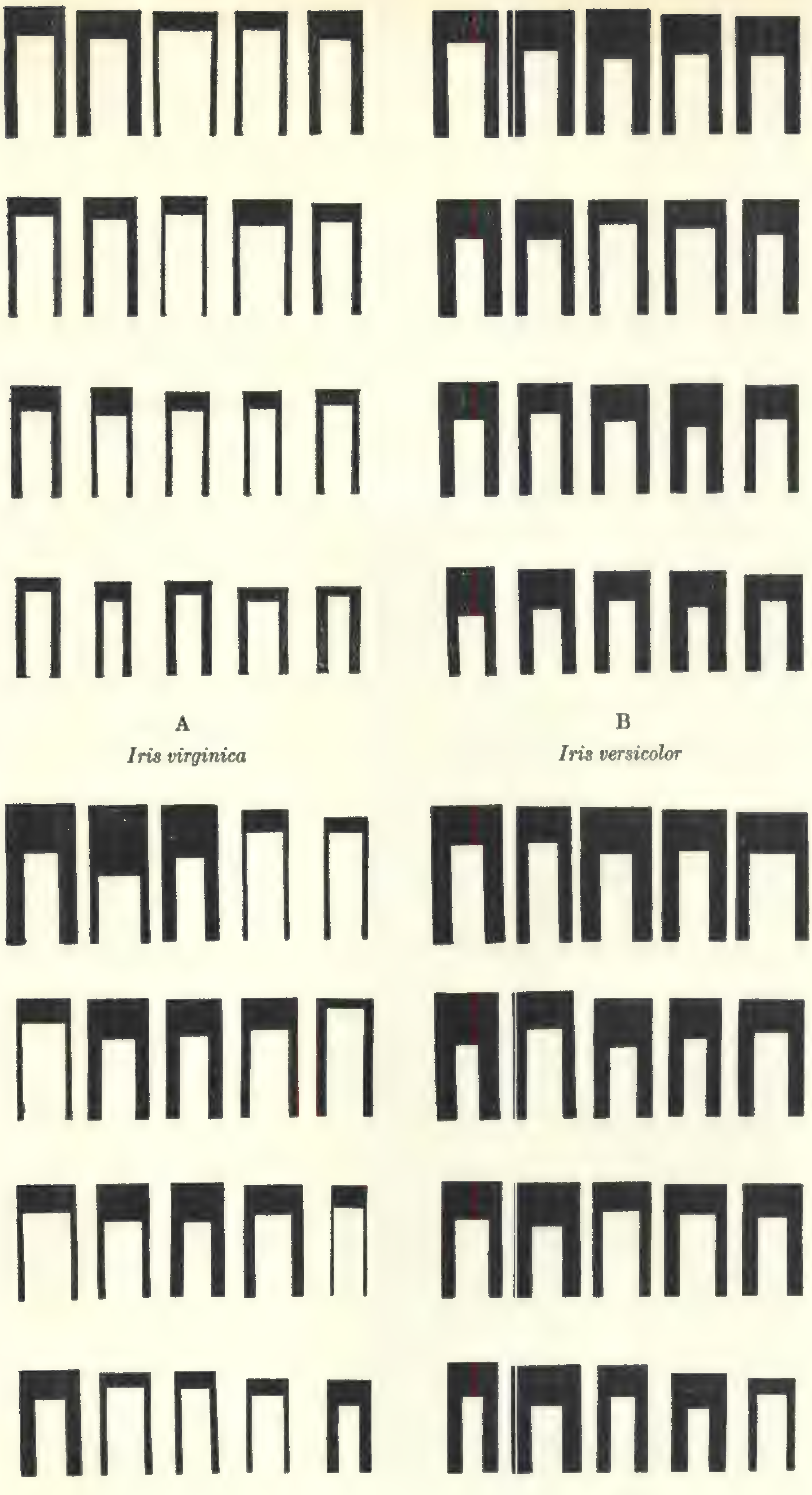
× **Iris robusta** E. Anderson,[1] new hybrid
(*Iris versicolor* × *I. virginica*)

Intermediate between *Iris versicolor* and *I. virginica*, but more robust; partially sterile.

V. Summary

The common blue flags of eastern North America are found to be made up of two separate and distinct species; a northern and

[1] **Iris robusta** E. Anderson
(*Iris versicolor* × *I. virginica*)
Virginicam et versicolorem intermedia sed robustior, partialiter sterilis.



A
Iris virginica

B
Iris versicolor

C
West St. Ignace, Mich.

D
Engadine, Mich.

Fig. 20. Ideographs of twenty individuals each of the two hybrid colonies studied: *C*, West St. Ignace, Mich.; *D*, Engadine, Mich.; above, average colonies of *I. virginica* and *I. versicolor* for comparison.

eastern one, *Iris versicolor* L., and a southern and a middle-western one, *Iris virginica* L.

Statistical studies have been made of 16 colonies of *Iris versicolor* and 39 of *Iris virginica.* Each species is found to be a natural group. In spite of wide variation within each species there is no tendency whatsoever for one to merge into the other, and the general average of each species is practically the same wherever it is studied. Although variation between individuals is met with in every colony examined it has not resulted in any appreciable regional differentiation, since the species in question moved into their present home at the close of the glacial period.

Iris versicolor and *Iris virginica* are kept separate in part by natural geographical barriers and in part by physiological differences which prevent them from being perfectly fertile with each other. Along the narrow zone where the two species come in contact hybridization occasionally takes place. Natural hybrids, closely resembling those produced experimentally, have been found at five points. At two of these localities hybrid populations of considerable size had arisen and have been studied in greater detail. There is some evidence that constant new forms might originate in this manner.

VI. Discussion

There are several objections which must be met before the above conclusions can be accepted as generally applicable. In the first place it might be argued that there were regional differences present within the two species which were not revealed because of the methods used, the characters chosen for study, etc. It is quite possible that such unrecognized differences existed, but if so they must have been of an entirely different order from the differences between species. The methods used *did* distinguish effectively between *Iris versicolor* and *Iris virginica* and did demonstrate that no such differences existed within either of the two species. For the material studied the conclusion therefore seems unavoidable that *the differences within species are of an entirely different nature from the differences between them.*

A more valid objection to the general application of the conclusions drawn in this work is that the two species belonged to an

old and well-defined genus and that different relations between species might be found to obtain in such a group as the genus *Aster*, for instance. From purely *a priori* reasoning it would seem quite possible that distinctions between species might be of a different nature in different parts of the vegetable kingdom. Conclusions drawn from a study of two species belonging to the Monocotyledons would certainly have to be confirmed with more closely related material before they could be accepted as valid for such a distantly related group as a genus of the Compositae.

Another hindrance to the general application of the conclusions reached in the study of these two species is the geophysical nature of the region in which they occur. It is without great barriers of any sort. With a greater degree of isolation, such as would occur in a region cut by great mountain chains, the differences *within* species might perhaps be very different. It would be particularly interesting to compare the regional differentiation of the closely related western species, *Iris missouriensis*.

LINNAEAN VS. JORDANIAN SPECIES

The main conclusion drawn from this investigation is that the Linnaean species is a natural and permanent group. It should therefore be the most effective one for purposes of classification. In regard to Jordanian species I am in complete agreement with Clausen ('27) when he says, "The old botanists worked according to their own common sense and delicate biological feeling, but they had a conception of species far more nearly coinciding with what we now arrive at by careful statistical observation of variation in the field and by cytological investigations and crossing experiments than our modern small-species taxonomists. 'Eine Art ist eine Art, ganz gleichgultig ob sie *Diapensia lapponica*, *Viola tricolor*, oder *Hieracium marginelliceps* heisst', says du Rietz. I quite agree that it is a matter of supreme indifference to Nature what *we* decide shall be the definition of a species. But it is by no means a matter of indifference to ourselves whether we accept or reject a form of nomenclature which obscures Nature's own chief system of division."

In my opinion those who have considered the Jordanon to be of prime importance, taxonomically and phylogenetically, have

ascribed undue significance to the fact that it comes true from seed. With more genetical or horticultural experience they would have realized that coming true from seed (homozygosity) is a mere corollary of the amount of inbreeding which has taken place and that it is of minor taxonomic and phylogenetic significance.

We can best demonstrate the actual significance of the Jordanon's true-breeding quality by examining the relationships between individuals in two different sorts of species; in one continuously cross-pollinated and in one continuously self-pollinated. These relations are diagrammed in fig. 21 at a and b. Let us take four individuals of a continuously cross-pollinated species, such a one as *Aster anomalus*, for instance, to name one that has actually been investigated (unpublished data). We may diagram these four individuals as **A**, **B**, **C**, and **D** (b, fig. 21) and if we examine them they will be found to possess certain inherent differences in such characteristics as the number, length, and shape of the ray flowers, the number and arrangement of the branches of the inflorescence, etc. Though two individuals may sometimes agree in a single characteristic, no two will possess the same combination of characters. In the next generation, however, none of these particular combinations will reappear. Plant **A** will be pollinated by pollen from other plants, as, for instance, by **B** as in the diagram, and the resulting offspring will show new combinations of characters unlike anything in the previous generation. In the diagram one of them is taken as an example and named **L**. Plants **M**, **N**, and **O** are similar new combinations arising from cross-pollinations between the other plants of the previous generation. There will be similar new recombinations of characteristics for each new generation. In other words, there will be just such a reshuffling of characteristics as occurs from generation to generation in human families; man being another species in which similar out-crossing prevails.

If we now turn to a self-pollinated Linnaean species and study the differences between individuals we will find that they are very similar to those studied in *Aster anomalus*. We may therefore diagram them similarly (a, fig. 21) as **A**, **B**, **C**, and **D**. In such a self-pollinated species, however, a single individual acts as father and mother for the next generation. There will ordinarily

be no crosses between A and B or B and C as there were in *Aster anomalus*. Furthermore, since such close inbreeding has obtained in the past, each individual will be practically homozygous (pure-breeding), and its progeny will resemble their parent and each other very closely. The seedlings of A will be so similar to their parent that they can be diagrammed as A, those of B will show the same combination of characters which distinguished B from A, C, and D, and may be diagrammed as B. This resemblance will continue from generation to generation as long as no cross-pollination occurs. Such a species is therefore divisible into a number of pure lines or Jordanons.

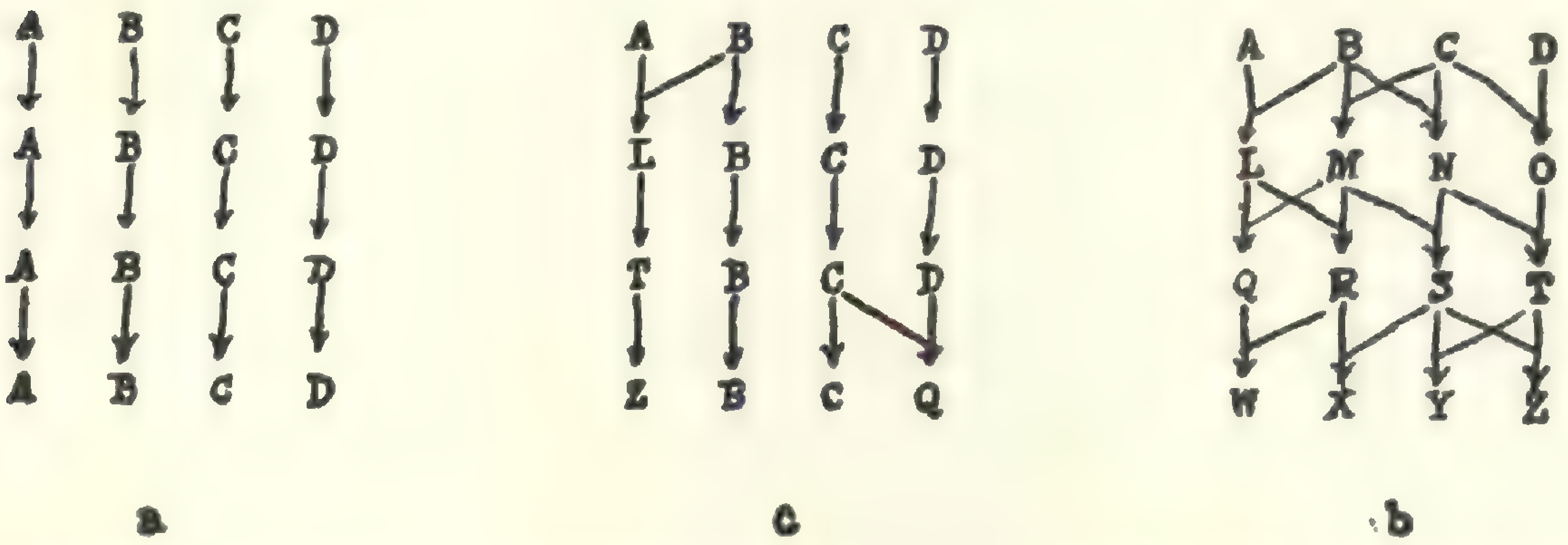


Fig. 21. Diagrammatic representation of the relationships between individuals in *a*, a self-pollinated species, *b*, a cross-pollinated species, and *c*, in *I. versicolor*.

It will be seen that the reappearance of distinctive combinations of characters from generation to generation is a mere corollary of the amount of inbreeding. Those Linnaean species which are continuously cross-pollinated will form new combinations in every generation. Those which are continuously self-pollinated will be divisible into recognizable pure lines or Jordanons. If species were of only these two sorts it might be possible to retain the Jordanon as an auxilliary unit, useful in the one case but not in the other. Unfortunately there is every transitional stage between the two extremes. *Iris versicolor* and *Iris virginica* are species of this intermediate sort. As has been shown above, *Iris versicolor* is usually self-pollinated though occasionally outcrossed. The relationships between individuals may therefore be diagrammed somewhat as in c of fig. 21. The diagram may be taken as typical of many species which can be only partially

separated into Jordanons. Those individuals, such as plants **A**, **B**, **C**, and **D** in the diagram, which have resulted from a long line of self-pollinations will give rise to true-breeding strains as long as they are self-pollinated. But when a cross-pollination occurs, as when **A** is crossed with **B**, it produces new recombinations of characteristics. In the diagram one of these new individuals, **L**, is taken as an example. Even though self-pollinated it will not breed true and its offspring will vary among themselves. One of them is represented in the diagram and named **T**. Plant **T** will likewise be too heterozygous to breed perfectly true, and its progeny must be given a new symbol in the diagram. So even though continuous self-pollination occurs among the progeny of the cross between **A** and **B**, it will take six or more generations before pure breeding Jordanons will be established.

Borrowing an idea from the diagrams in fig. 21, we may think of each species as a net, with the knots representing individuals. Those species in which cross-pollination regularly obtains will have a very short mesh, interweaving from one generation to the next. Those species, such as *Iris versicolor,* in which it is rare, will have a much longer mesh with fewer connecting cross-threads. Some few species will be so seldom cross-pollinated as to seem hardly net-like in their make up. They will be more like separate and unconnected knotted strings, but it is to be doubted if even in such extreme cases there never occurs a cross-pollination which brings the strings of the net together. Even though they occurred on the average only once in forty or fifty generations, it would cause the ultimate interweaving of the whole net and the disappearance of the single strings as separate units.

The case for the Jordanon as a universally applicable unit becomes even more absurd when we consider the case of a species which is cross-pollinated in one part of its range and self-pollinated in another. While this has not been demonstrated for any wild species, there is no *a priori* reason why such a delicately balanced relation might not vary under different environments. Leighty and Taylor ('27) have called attention to the fact that this has actually occurred in wheat which has different percentages of natural outcrossing in different parts of the world, as, for instance, in the Punjab where Howard and Howard ('09) report a very high

percentage. It has been found for numerous species that they are cross-pollinated only by a single insect. Such a Linnaean species, cross-pollinated in one part of its range and self-pollinated in another, would be divisible into Jordanons in the latter region but not in the former.

The division of a Linnaean species into Jordanons is therefore seen to be a mere corollary of the amount of inbreeding which has obtained in that species. Where Jordanons do occur they owe their existence to continuous self-pollination and their individuality disappears as soon as a cross-pollination takes place. In those species where cross-pollination is of rare occurrence they will undoubtedly persist for some time, perhaps even for centuries, but they will ultimately disappear.

These studies have shown that the Linnaean species, on the other hand, may retain its individuality, though submitted to widely differing environments, for long periods of time. *Iris versicolor* and *Iris virginica*, for instance, must have persisted as recognizable units since they spread into their present homes at the close of the glacial period. Important as the Jordanon may be in the case of cultivated plants, or in those Linnaean species in which it naturally occurs, it is a relatively temporary unit of little taxonomic or phylogenetic significance.

There remains to consider the bearing of the studies reported above on the question of the origin of species. For the material studied it has been shown that *the differences between species are of an entirely different order from the differences between individuals.* There is no evidence that these differences between individuals might, under the influence of natural selection or of any other natural force, eventually be compounded into differences comparable to those between the two species studied. This conclusion is not in accord with most current speculation on the subject. Since the time of Darwin it has been very commonly supposed that the processes which give rise to differences between individuals, if allowed to operate over a longer period, will produce specific differentiation. This general theory has gone through many phases as biology has advanced; in its most recent form it is held by many of the Drosophila workers who see in the gene mutation the unit process which, compounded a thousand-fold, results in specific differences.

There is little in the evidence reported in this paper to support such an explanation of the origin of species. If all the individual differences which have occurred in *Iris virginica* since the glacial period have not produced recognizable regional differences within the species, the production of new species by this means must be a very slow process.

If we are to deny the slow accumulation of individual differences an important role in species building, to what process are we to turn? A number of recent investigators, Brieger ('28) Clausen ('27), Karpechenko ('27), to name only a few, have reported the experimental production of true-breeding hybrids as the result of new chromosomal realignments. The careful experimental investigation of these hybrids has strengthened the case of those who believe with Lotsy ('16) that hybridization has been an important factor in the evolution of species. Though it has not been investigated cytologically, the colony studied at Engadine is apparently composed of similar true-breeding hybrids of natural origin. While it will have to be very thoroughly investigated before it can be taken as conclusive, this apparent example of a new and constant form produced by the hybridization of two separate species is certainly very suggestive.

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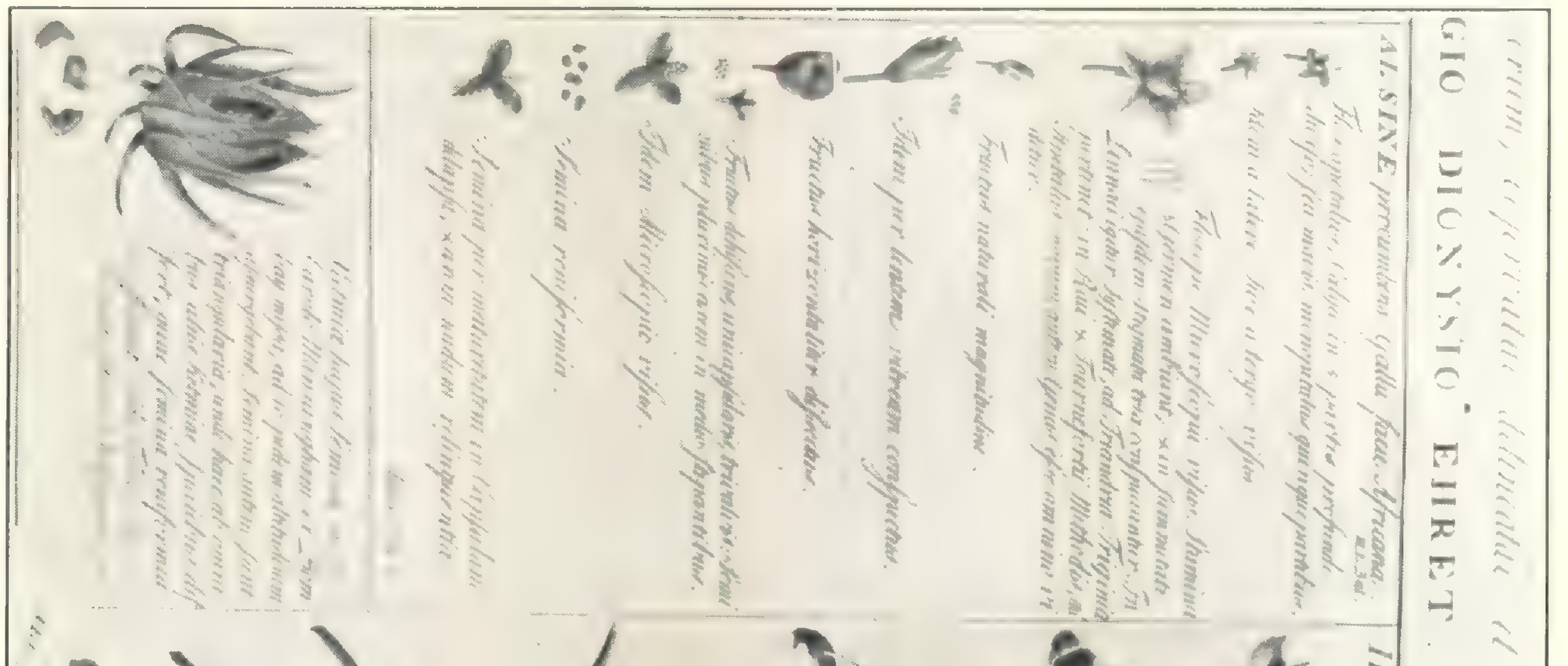
Explanation of Plate

PLATE 35

Fig. 1. *Iris latifolia Virginiana*, etc. Miller. From Ehret, G. D., Plantae Depictae, Tab. VI. 1748.

Fig. 2. *Iris latifolia Virginiana* etc. Miller. From Ehret, G. D., Plantae Depictae, Tab. VIII. 1748.

1



2

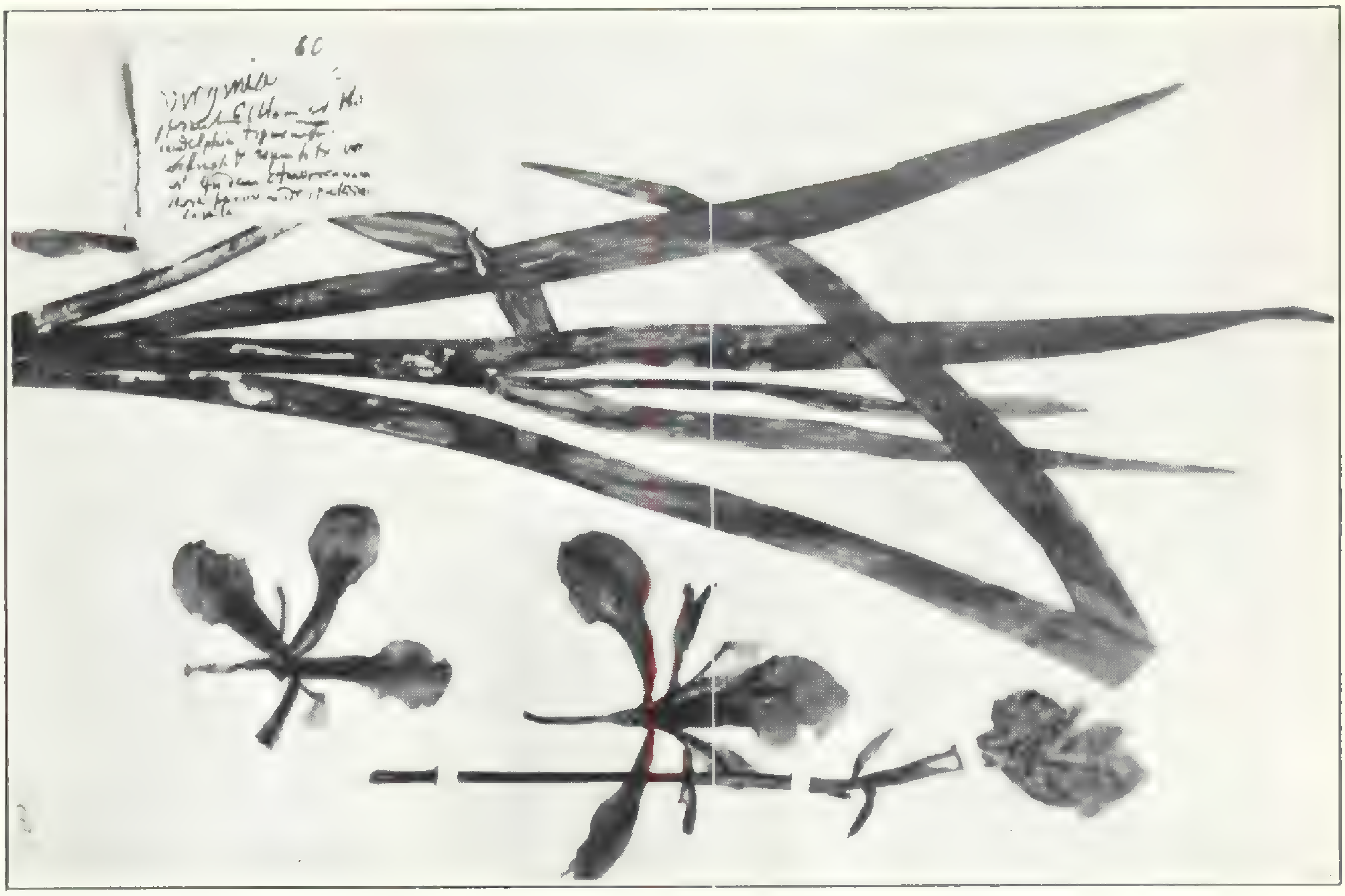
ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 36

Fig. 1. *Iris versicolor* L. Dillenius' specimen of *Iris americana versicolor*, etc. deposited in the Dillenian Herbarium at Oxford.

Fig. 2. *Iris carolina* Radius. From Radius, W. M., Naturforsch. Ges. Leipzig Schrift. **1:** 158. taf. III.



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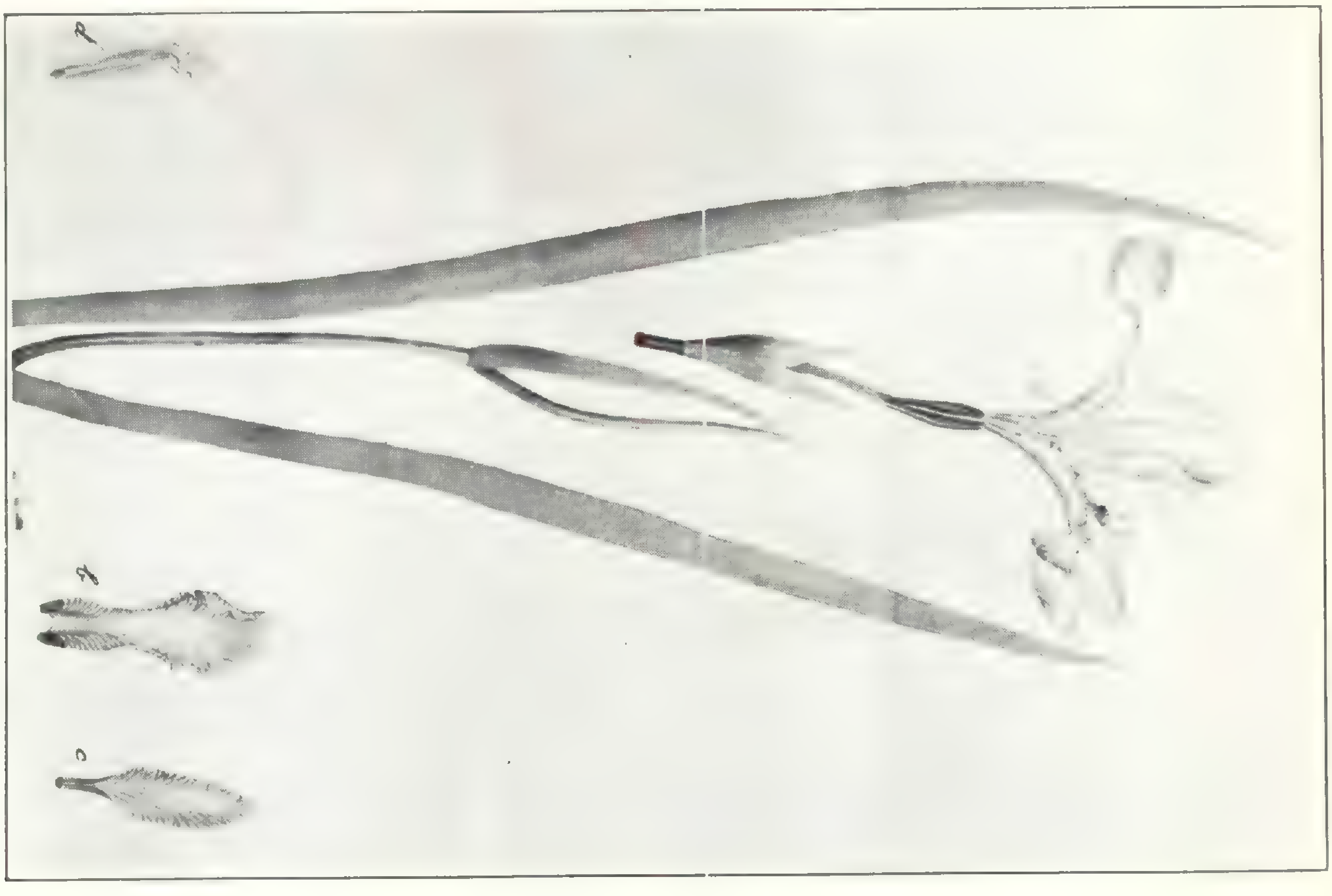


2

ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 37

Flowers of *Iris virginica*, × 1/3

Fig. 1. Plant ABC—collected at Orchard Farm, Mo.
Fig. 2. Plant ABC—collected at Orchard Farm, Mo.
Fig. 3. Plant ABC—collected at Orchard Farm, Mo.
Fig. 4. Plant ABC—collected at Orchard Farm, Mo.
Fig. 5. Plant ABC—collected at Orchard Farm, Mo.
Fig. 6. Plant ABE—collected at Fort Madison, Ia.
Fig. 7. Plant ABE—collected at Fort Madison, Ia.
Fig. 8. Plant ABE—collected at Fort Madison, Ia.
Fig. 9. Plant ABQ—collected at Gilbertville, Ia.

ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 38

Flowers of *Iris versicolor*, × ⅛

Fig. 1. Plant ABY—collected at Cohasset, Mass.
Fig. 2. Plant ACF—collected at New Haven, Conn.
Fig. 3. Plant ACF—collected at New Haven, Conn.
Fig. 4. Plant BBG—collected at Harmonsburg, Pa.
Fig. 5. Plant collected at Cedar Lake, Nova Scotia.
Fig. 6. Partial albino, var. "Stella Main"—collected in Connecticut.
Figs. 7–9. Seedlings grown at the Missouri Botanical Garden from seed collected at Connecticut Lakes, N. H.

ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 39

Flowers of *Iris virginica*, × ⅓.

Figs. 1–2. Plant ABB—collected at Valley Park, Mo.
Fig. 3. Plant ACZ—collected at Fish Creek, Wis.
Fig. 4. Plant ABT—collected at Yale, Mich.
Fig. 5. Plant ABT—collected at Yale, Mich.
Fig. 6. Plant ABT—collected at Yale, Mich.
Fig. 7. Plant ABP—collected at Otisville, Mich.
Fig. 8. Plant ABP—collected at Otisville, Mich.
Fig. 9. Plant ABP—collected at Otisville, Mich.

ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 40

One flower each of five sister plants of *Iris versicolor* grown at the Missouri Botanical Garden from a seed capsule collected at Connecticut Lakes, N. H.

ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 41

A comparison of *Iris versicolor* and *Iris virginica* with *Iris × robusta*, the hybrid between them.

Top row, immature capsules with one locule exposed.

Middle row, immature capsules.

Bottom row, flowers.

In each case the specimen at the left is from plant IAAG (*Iris versicolor*), that at the right from IAAA-3 (*Iris virginica*), and that in the center from their hybrid IXAM (*Iris × robusta*).

ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 42

Fig. 1. Typical flower stalk of *Iris virginica.*
Fig. 2. Typical flower stalk of *Iris versicolor.*
Fig. 3. *Iris virginica* photographed at Huntingdon, Tenn.
Fig. 4. *Iris virginica* photographed at Wilmington, N. C.

1

2

3

4

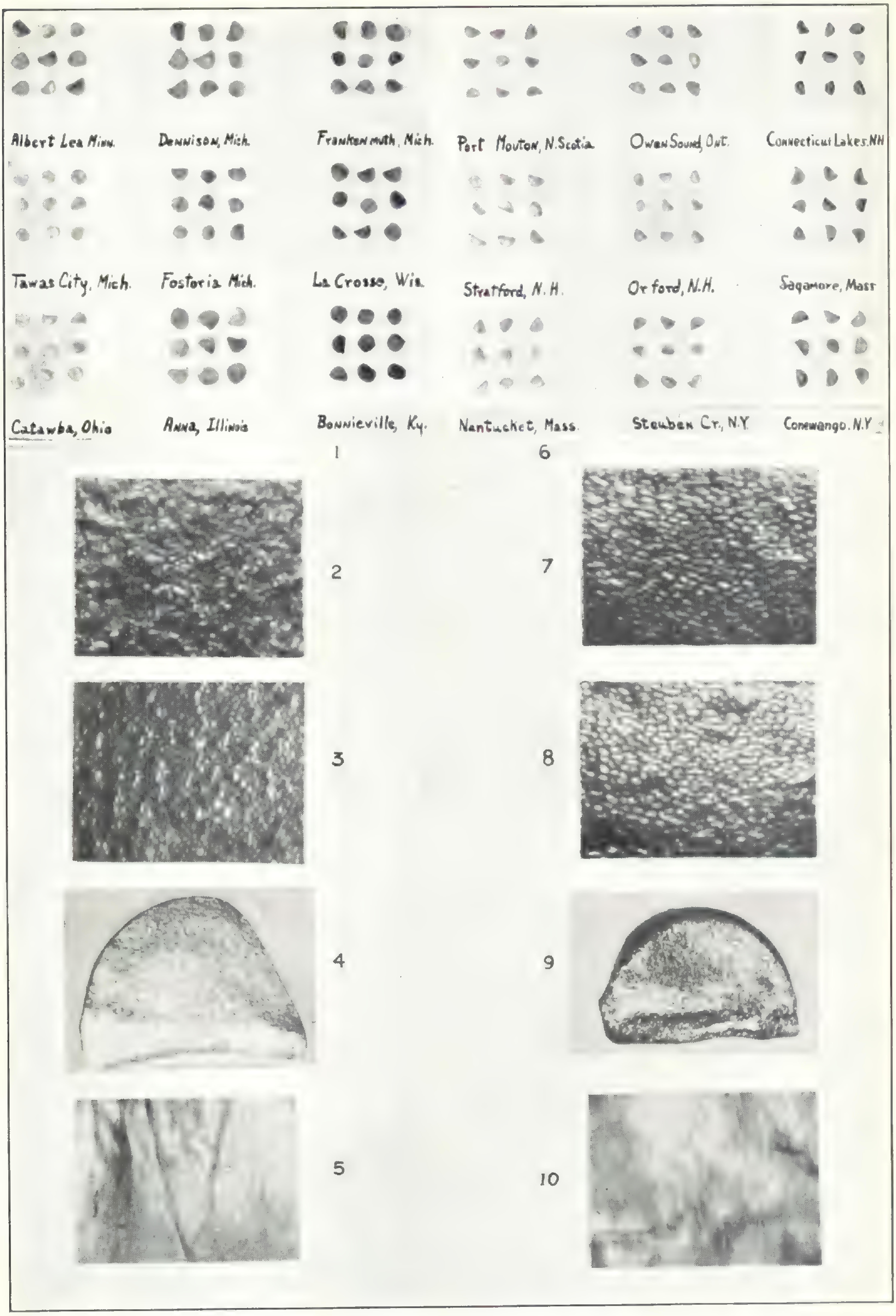
ANDERSON—PROBLEM OF SPECIES IN IRIS

Explanation of Plate

PLATE 43

Figs. 1–5. *Iris virginica.*
- Fig. 1. Collected seeds from nine localities, × ½.
- Fig. 2. Seed surface (St. Louis, Mo.), × 30.
- Fig. 3. Seed surface (Catawba, Ohio), × 30.
- Fig. 4. Seed, × 7.
- Fig. 5. Lining of seed capsule, × 30.

Figs. 6–10. *Iris versicolor.*
- Fig. 6. Collected seeds from nine localities, × ½.
- Fig. 7. Seed surface (Sagamore, Mass.), × 30.
- Fig. 8. Seed surface (Conewango, N. Y.), × 30.
- Fig. 9. Seed, × 7.
- Fig. 10. Lining of seed capsule, × 30.



ANDERSON—PROBLEM OF SPECIES IN IRIS

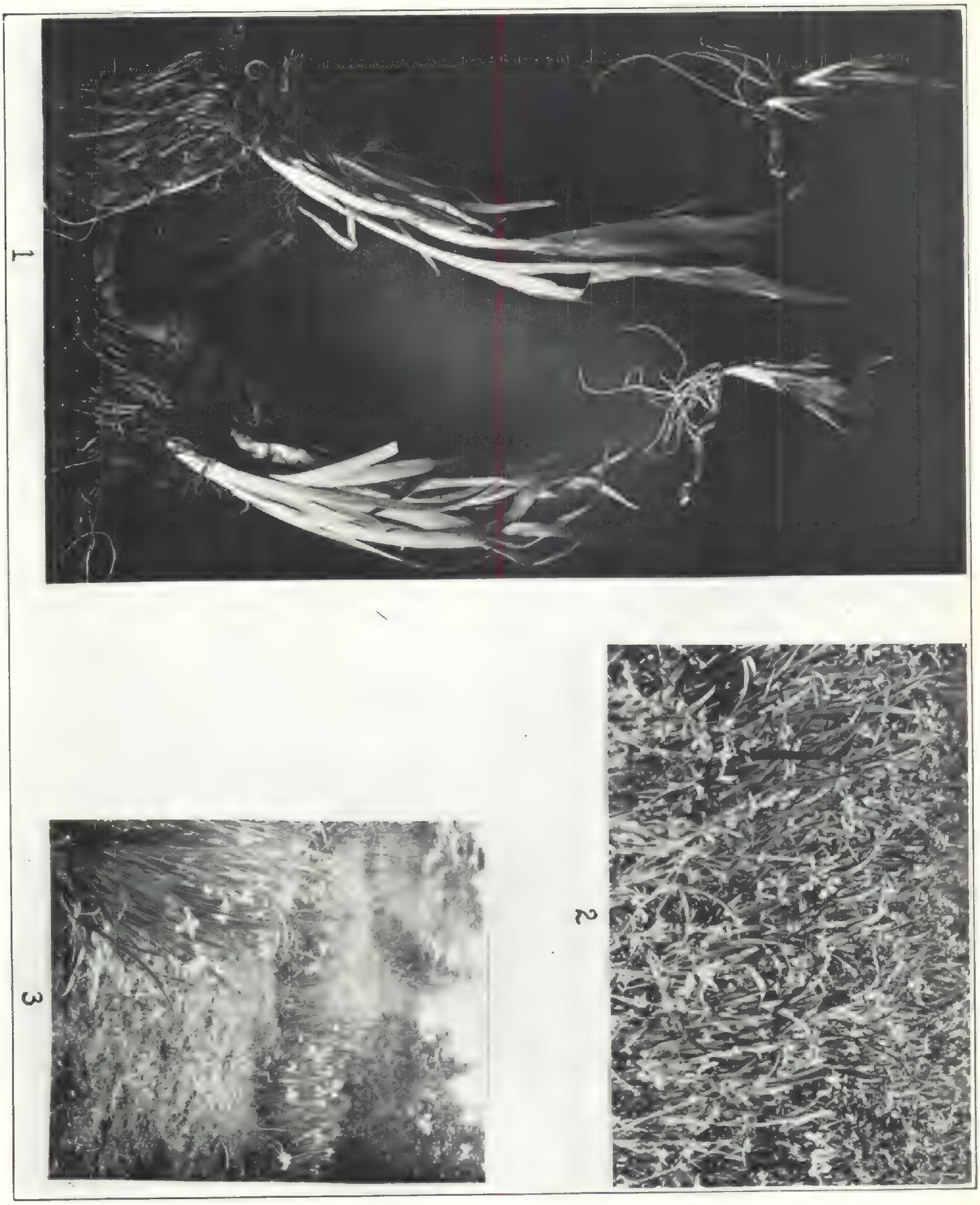
Explanation of Plate

PLATE 44

Fig. 1. Upper row, two plants of *Iris virginica* from Valley Park, Mo., grown in cinders along railroad track; lower row, two plants from the same colony but growing in rich swamp.

Fig. 2. Large single clone of *Iris virginica*, Maysville, N. C.

Fig. 3. Colony of *Iris virginica* at Camden, Tenn.



ANDERSON—PROBLEM OF SPECIES IN IRIS

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A NEW VARIETY OF VERNONIA LINDHEIMERI[1]

ESTHER L. LARSEN

Instructor in Botany in the University of Montana
Formerly Jessie R. Barr Fellow in Botany, Washington University

A very interesting *Vernonia* was collected by Roxana S. Ferris and Carl D. Duncan along the Sanderson-Sheffield Road, twelve miles from Sanderson, Terrell County, Texas, July 19, 1921. The plant was distributed as *Vernonia Lindheimeri* Gray & Engelmann; but upon critical study and comparison with a relatively large suite of specimens representing this species in the Missouri Botanical Garden Herbarium, the Ferris and Duncan plant shows such marked variation from the type of the species that it seems worthy of recognition as an outstanding variety. A description is recorded as follows:

Vernonia Lindheimeri Gray & Engelmann var. **leucophylla** Larsen, n. var. Pl. 45.

Formae typicae habitu simili; foliis utrinque dense albido-tomentosis; involucri squamis lineari-lanceolatis, acutis, dense tomentosis, marginibus purpurascentibus; achaeniis circiter 4 mm. longis, glabris.

Suffruticose, stem densely tomentose; leaves linear to linear-lanceolate, 4–16 cm. long, 3–8 mm. broad, entire, densely tomentose on both surfaces, margins of the younger leaves occasionally revolute; inflorescence terminal, branching, spreading, leafy; heads 12–17 mm. high; involucre broadly campanulate, 4–5-seriate, 8–9 mm. high and 8–10 mm. in diameter; bracts linear-lanceolate, acute, purple-margined and densely tomentose; heads 50–60-flowered; flowers purple; pappus white; achenes

[1] Issued December 22, 1928.

about 4 mm. long, glabrous and glandless or rarely bearing a few glands in the furrows.—Texas: collected along the Sanderson-Sheffield Road, twelve miles from Sanderson, Terrell County, July 19, 1921, *Roxana S. Ferris & Carl D. Duncan 2826* (Mo. Bot. Gard. Herb. No. 902145 type).

Vernonia Lindheimeri Gray & Engelmann has been recorded heretofore only from Texas. It is noteworthy, however, that specimens of this species were collected in pine woods about Texarkana, Arkansas, August, 1881, by the late Mr. George W. Letterman. This collection extends considerably the geographical range of the species, which, from material in the Missouri Botanical Garden Herbarium, may now be given as from southern Arkansas in the region of Texarkana southwestward to Sweetwater and San Antonio, Texas.

The variety *leucophylla* at the present time is known only from Terrell County, Texas, which is about 200 miles west of the westernmost station recorded for the species. The distribution areas of *Vernonia Lindheimeri* and its variety *leucophylla* in all probability on further exploration will be found to overlap.

Explanation of Plate

PLATE 45

Vernonia Lindheimeri Gray & Engelmann var. *leucophylla* Larsen
Texas

From the type specimen, *Ferris & Duncan No. 2826*, in the Missouri Botanical Garden Herbarium.

LARSEN—NEW VARIETY OF VERNONIA LINDHEIMERI

DYSOSMA: A NEW GENUS OF BERBERIDACEAE[1]

ROBERT E. WOODSON, JR.

Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

While examining herbarium material of the genus *Podophyllum* in the Gray Herbarium of Harvard University recently, the writer happened upon six sheets of a very curious plant collected in China by Henry in 1854, and also two sheets of similar specimens collected by Ford, and distributed from the Hongkong Botanic Garden in 1885.

The plants were immediately perceived to be radically distinct from both the North American *P. peltatum* L. and the Asiatic *P. Emodi* Wall. The evident differences are larger size in general, much broader leaves with very shallow and regular lobing, and especially an umbel of four to nineteen flowers instead of the familiar solitary flower of the more common species. Upon a consultation of the literature, it was found that the plants correspond to the description of *P. versipelle* Hance.

A somewhat closer superficial examination disclosed the facts that the pedicels of the inflorescence are distinctly recurved, while those of the more familiar species are erect or slightly nodding, and that the petals are also drooping, oblong-lanceolate in outline, and of a dull reddish color. A difference in the rhizome was also evident, it being thick and fleshy and destitute of scales, with the nodes crowded together almost as a tuber, while the rhizomes of both *P. peltatum* and *P. Emodi* are more like the ordinary creeping stem, if such a distinction can be made, being slender, more fibrous, and giving rise to a conspicuous production of cataphyllary scales (pl. 46, figs. 5 and 10).

Dissections of the species in question disclosed further facts of considerable interest. The stamens of *P. versipelle* are four to six in number, fewer than in the other species, and are about one-half again as large in every dimension as those of both *P peltatum* and *P. Emodi*. The filaments are sharply curved

[1] Issued December 22, 1928.

away from the pistil, unguiculate in a certain manner, and the sterile connective is greatly developed, apiculately produced at the apex, and bears the thin locules conspicuously extended in a parallel position from its ventral side. The anthers, moreover, are introrse, one of the most striking features of the species, since the anthers of all other Berberidaceae are extrorse, including those of *P. peltatum* and *P. Emodi* which are also produced laterally from a narrow connective upon straight filaments. Upon an examination with a compound microscope the pollen of *P. versipelle* was found to be perfectly spherical, and about one-half to two-thirds the size of the lobed pollen of *P. peltatum* and *P. Emodi*.

The pistil of *P. versipelle* also produces a definite slender style bearing a globose stigma, while the other two species have peltate stigmas which are sessile or only slightly elevated. The mature fruit of *P. versipelle* is unknown, but it is presumed to be rather similar to the pulpy bacca of *P. peltatum* and *P. Emodi*.

With two such distinct elements as are represented by *P. versipelle*, on the one hand, and *P. Emodi* and *P. peltatum*, on the other, it appears that the equilibrium of the Berberidaceae and the tribe Podophylleae, containing at present only the genus *Podophyllum*, should be more easily maintained by recognizing the elements as distinct genera of a single tribe, since two such genera would be quite as distinct in their separate tribe as those of the other tribes of the family, as, for instance, *Berberis* and *Mahonia*, and *Epimedium* and *Vancouveria* in the Berberideae.

In establishing the new genus, the name *Dysosma* has been constructed from the Greek δῦς + ὀσμή, signifying "a disagreeable odor," chosen arbitrarily upon the testimony of Hance, who was able to examine fresh plants, and who pronounced their odor as most remarkably putrid.

Tabulated, the differences of *Dysosma* and *Podophyllum* have been found to be as follows:

DYSOSMA	PODOPHYLLUM
Rhizome tuberous, without cataphyllary scales or prophylls.	Rhizome a creeping slender stem, with both cataphyllary scales and prophylls.
Flowers in umbels.	Flowers solitary.

DYSOSMA	PODOPHYLLUM
Pedicels reflexed.	Pedicels erect or only slightly nodding.
Petals drooping, dull reddish.	Petals spreading, white.
Pistil with a definite style.	Pistil without a definite style.
Stigma globose.	Stigma peltate.
Stamens 4–6, introrse.	Stamens 6–18, extrorse.
Stamens with an enlarged sterile connective.	Stamens without an enlarged sterile connective.
Filaments unguiculate, spreading away from the pistil.	Filaments straight, not spreading.
Leaf-lobes shallow and regular, sharply and regularly denticulate.	Leaf-lobes deep and irregular, entire or irregularly laciniate.
Pollen spherical, relatively small.	Pollen lobed, relatively large.

An examination of the literature of the many-flowered Podophyllums published from Asia discloses the fact that six species have been described, differing from one another by dissimilarities strikingly analogous to those variable characteristics frequently found in *P. peltatum* and *P. Emodi*,[1] such as the position of the flowers, pubescence, lengths of stamens, and even carpellary number. The specific features of *P. Veitchii* and *P. difforme*, for example, are stamens slightly longer than the petals, and stamens half as long as the petals, respectively; supposed to differ from *P. versipelle*, which is presumed to have stamens and petals of equal length. Upon examination of herbarium[2] material the writer has been fortunate to find a specimen with two flowers remaining upon the pedicels of the inflorescence, one with stamens longer, and the other with stamens somewhat shorter than the petals (*Henry 5372F*, MBG). Likewise, petals have been found to be notched in a manner similar to that described for *P. Onzoi*. *P. Esquirolii*, furthermore, is said to

[1] A paper dealing with the morphological variability and the involved synonymy which it has produced in the genus *Podophyllum* is now in manuscript.

[2] In the taxonomic treatment which follows, the herbaria from which exsiccatae have been cited are abbreviated as follows: Gray Herbarium (GH); Missouri Botanical Garden Herbarium (MBG); New York Botanical Garden Herbarium (NY); United States National Herbarium (US). The writer desires to express his appreciation for the facilities which were kindly allowed him by the respective curators of each.

have leaves which are almost without lobing, a feature which might be explained by the great leaf variability of *P. peltatum* and *P. Emodi*. Although predominately extra-axillary, the inflorescence of *Dysosma* has been occasionally found to be axillary. Although perhaps taking too much liberty in doing so, it has been thought advisable in the establishment of the new genus to treat the species described upon such characters as have been found spontaneously variable in *P. peltatum* and *P. Emodi* as representing variations of a single species. Since axillary forms have been reported only from Formosa, it may well be that the position of the umbel is not variable and that the axillary forms are specific. Until better knowledge is available, however, the extra-axillary form is taken as the normal, and the axillary as the abnormal form. Although future study may hold other species genuine, only one, the oldest, which happens to be *P. pleianthum* Hance, has been retained and transferred to *Dysosma*.

Dysosma[1] n. gen.

Herbaceous caulescent perennial, glabrous or somewhat pubescent. Rhizome indeterminate, thickened, fleshy, without cataphyllary scales or prophylls. Leaves 1 or 2, peltate, palmately lobed, the lobes regular, usually 6 large anterior and 2 smaller posterior lobes, regularly denticulate. Flowers in axillary or extra-axillary umbels of 4–19, the pedicels reflexed. Petals usually 6, oblong-lanceolate, dull reddish, drooping. Sepals 3, petaloid, fugaceous. Stamens usually 6; filaments long, unguiculate, spreading from the pistil; anthers 2-celled, dehiscing longitudinally, ventrally parallel, produced from an enlarged

[1] Dysosma Woodson gen. nov. Berberidacearum, herba perennis caule erecto glaberrimo pruinoso 3–5 dm. alto; foliis radicalibus solitariis caulinis binis crassiusculis centrice vel subcentrice peltatis orbiculatis palmatim 6–8-lobatis, lobis late triangulo-oblongis acuminatis vix quintam diametri partem aequantibus, margine creberrime subulato-denticulatis, petiolis pruinosis aequilongis; pedicellis declinatis; floribus 4–19 ad apicem caulis infra foliam superius petiola vel inter folia apice caulis nascentibus, ebracteatis; sepalis 3 tantam deciduis; petalis 6–9 oblongis acutis sordide sanguineo-rubris 1.5 cm. longis; stamine 4–6 antheris valvula longitudinali utrinque dehiscentibus introrsis, filamentis unguiculatis aequilongis connectivo ultra loculos in apiculum producto; ovario ellipsoideo-sphaerico gracilibus stigmateque globosis cristatis coronatis, ovulis indefinitis.

apiculate sterile connective, introrse. Ovary oblong in outline, 1-celled; ovules many, anatropous, each enclosed in a fleshy aril, disposed upon a lateral placenta; stigma globose, thick, produced upon a definite style. Mature fruit unknown, probably a fleshy berry. Type, *Henry 5372F*, Sze-chuan, China, 1885–88 (MBG).

Type species: *Dysosma pleiantha* (Hance) Woodson.

1. **Dysosma pleiantha** (Hance) Woodson, n. comb. Pl. 46.

Podophyllum pleianthum Hance, Jour. Bot. **21**: 175. 1883.

Podophyllum versipelle Hance, *l. c.* 362. 1883.

Podophyllum Veitchii Hemsl. & E. H. Wils., Kew Bull. Misc. Inf. **1906**: 152. 1906.

Podophyllum difforme Hemsl. & E. H. Wils., *l. c.* 1906.

Podophyllum Esquirolii Léveillé in Fedde, Repert. **11**: 298. 1912.

Podophyllum Onzoi Hayata, Icon. Pl. Form. **5**: 2. 1915.

Characters of the genus.

Distribution: southeastern China and the island of Formosa.

Specimens examined:

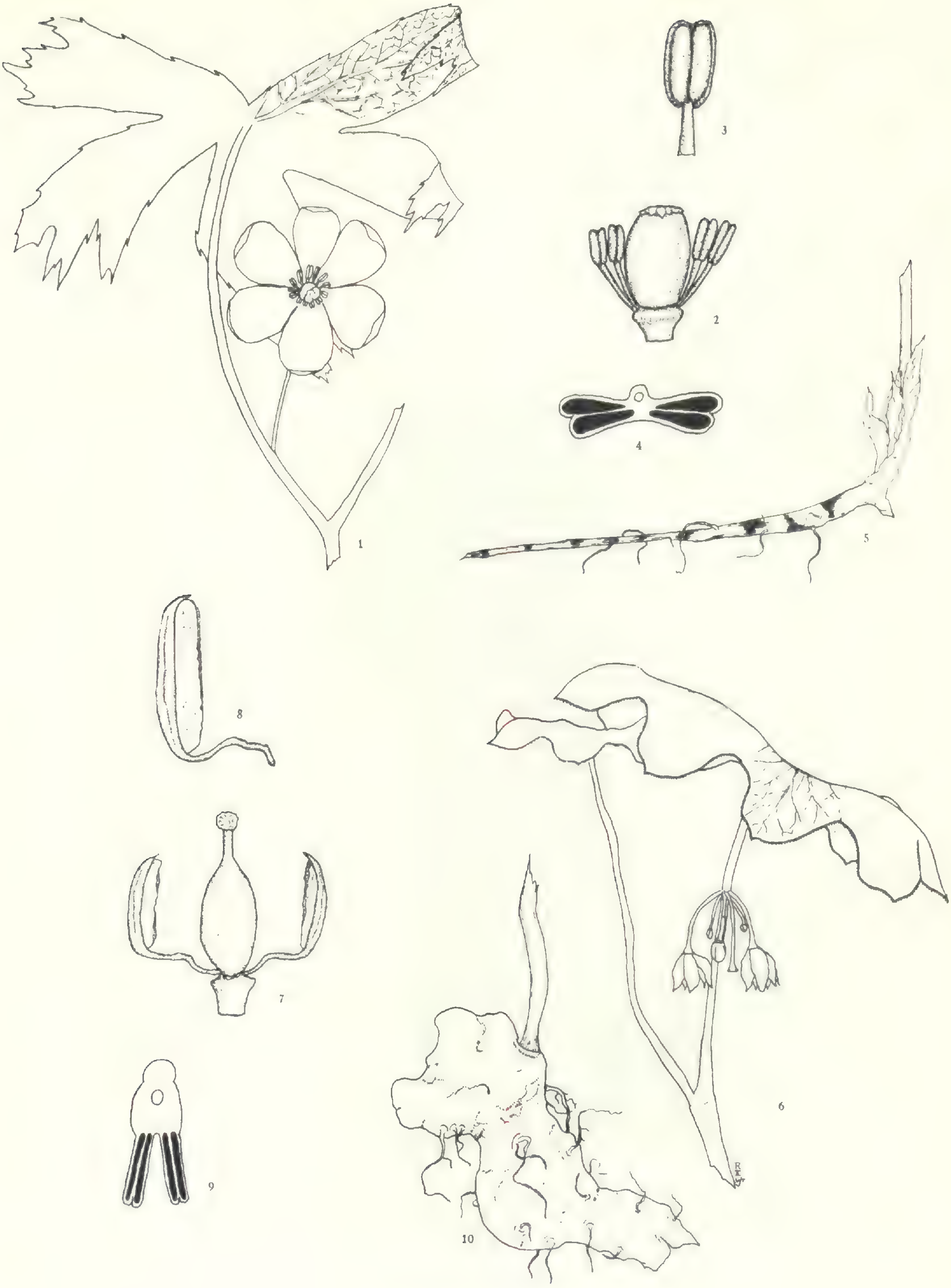
China: Hupeh, April, 1885, *Henry 3952* (GH, US); data lacking, Hongkong Botanic Garden, *Ford* (GH); Canton, Lo-fanshan Mts., date lacking, *Ford 1092* (US); Sze-chuan, 1885–88, *Henry 5372* (GH, MBG type, NY, US); Chekiang, 1903, *Barchet 24* (US); Chekiang, 1906, *Barchet* (US); western Hupeh, May, 1907, *Wilson 3202* (US).

Explanation of Plate

PLATE 46

Comparative morphology of *Podophyllum* and *Dysosma*.

Fig. 1. Habit of *Podophyllum Emodi* Wall.
Fig. 2. Receptacle of *P. Emodi* with pistil and four stamens.
Fig. 3. Stamen of *P. Emodi.*
Fig. 4. Diagrammatic cross-section of stamen of *P. Emodi.*
Fig. 5. Rhizome of *P. Emodi.*
Fig. 6. Habit of *Dysosma pleiantha* (Hance) Woodson.
Fig. 7. Receptacle of *D. pleiantha* with pistil and two stamens.
Fig. 8. Stamen of *D. pleiantha.*
Fig. 9. Diagrammatic cross-section of stamen of *D. pleiantha.*
Fig. 10. Rhizome of *D. pleiantha.*



WOODSON—DYSOSMA

STUDIES IN THE APOCYNACEAE. II[1]

A Revision of the Genus Stemmadenia

ROBERT E. WOODSON, JR.

Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

Historical Review

The Apocynaceous genus *Stemmadenia* was established in 1844 by Bentham,[2] who recognized three species, the type, *S. glabra*, *S. pubescens*, and *S. mollis*. The first and third species were entirely new to science, but the second Bentham perceived to be identical with *Bignonia ? obovata* Hook. & Arn.,[3] although he chose to give the species an original name. The specific adjective of Hooker and Arnott has subsequently been restored by Schumann.[4]

In 1853, A. Richard,[5] evidently unaware of Bentham's genus, published the genus *Odontostigma,* with one species, *O. Galeottiana*, from the environs of Havana, Cuba. From the evidence of an excellent plate which illustrates Richard's genus, Miers,[6] in 1878, was able to definitely identify *Odontostigma* as representing merely another element of *Stemmadenia.*

Thirty-four years after the establishment of the genus by Bentham, Miers[7] presented a treatment of *Stemmadenia* in his monograph of the South American Apocynaceae. In the treatment of Miers, besides the three species of Bentham, five new

[1] Studies in the Apocynaceae. I, containing an historical account of the taxonomy of the family and a critical study of the tribe Apocyneae, is in manuscript, and will appear in a subsequent number of the Annals of the Missouri Botanical Garden.

[2] Benth. Bot. Voy. Sulph. 124. *t. 44.* 1844.

[3] Hook. & Arn. Bot. Beechey's Voy. 439. 1841. Concerning the mistake of the *Stemmadenia* for a *Bignonia*, Bentham wrote: "A portion of the seed vessel and seeds of a *Pithecoctenium*, probably *P. muricatum*, had been by mistake laid by Dr. Sinclair into the same sheet with the specimen of this plant, and had misled the authors of the 'Botany of Captain Beechey's Voyage' and induced them to refer the plant doubtfully to *Bignonia*." Benth., *l. c.* 125. 1844.

[4] K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**^{2}: 149. 1895.

[5] A. Rich. in Sagra, Hist. Cub. **11**: 868. *t. 56.* 1853.

[6] Miers, Apoc. S. Am. 76. 1878.

[7] *l. c.* 74–77. 1878.

Issued December 22, 1928.

species are added to the genus, namely, *S. grandiflora* (*Tabernaemontana grandiflora* Jacq.), *S. insignis*, *S. Galeottiana* (*Odontostigma Galeottiana* A. Rich.), *S. bella*, and *S. bignoniaeflora* (*Echites bignoniaeflora* Schl.). Of these, the most important by all means is *S. grandiflora*, which introduced a very distinct element into the genus and which, in this revision, is considered to merit subgeneric distinction.

The work of Miers, which was the last to review the genus, was largely but a compilation of the descriptions of plants which the author himself had never seen, and since he had been able to examine only three of the eight species which he recognized, his product is liable to frequent errors, to obviate which will be in part the duty of this revision.

Since the treatment of Miers, several species have been added to the genus, and explorative activity in Central and South America has greatly augmented representatives of the genus in herbaria. In the course of recent determinative work on miscellaneous American Apocynaceae, an encounter with the technical and nomenclatoral difficulties of *Stemmadenia* has convinced the author that a revision of the genus might appropriately be introduced into this series of Studies in the Apocynaceae.

The study entailed in the preparation of this revision was begun at the Gray Herbarium of Harvard University and completed at the herbarium of the Missouri Botanical Garden. The author desires to express his appreciation to Dr. B. L. Robinson and to Dr. J. M. Greenman for assistance and suggestions during the course of the study, and to Dr. George T. Moore for the privileges of the Missouri Botanical Garden. He is also indebted to Dr. N. L. Britton and Mr. Percy Wilson, of the New York Botanical Garden, Dr. F. W. Pennell, of the Philadelphia Academy of Natural Sciences, Dr. W. R. Maxon and Mr. E. P. Killip, of the United States National Herbarium, and to Mr. P. C. Standley and Mr. J. F. Macbride, of the Field Museum, for the courtesy of study in the various herbaria.

General Morphology

The various species of *Stemmadenia* are shrubs or small trees attaining a height of two to twelve meters.

Leaves.—The leaves of the genus are opposite, membranaceous, entire, penninerved, glabrous or pubescent, and petiolate. The sheaths of the petioles are conspicuous, meeting in a shallow ring about the stem. Numerous fusiform glands are concealed in the petiolar ring of the leaves, but are fully exposed and persistent when the leaf drops from the stem. The presence of these glands has been overlooked by each previous student of the genus.

The outline of the leaf varies little, the most frequent form being ovate-oblong. However, variations occur in the spathulate leaves of *S. Donnell-Smithii* and the lanceolate leaves of *S. eubracteata.* The surface of the leaves is extremely variable, and may grade upon the same specimen of certain species from tomentose, through barbate, to glabrous. In the case of other species, however, the surface of the leaves is relatively constant.

The length of the petiole appears of some constancy, and is occasionally used as an accompanying taxonomic criterion.

Inflorescence.—The inflorescence is a reduced terminal cyme, bearing from one to several flowers usually, and three inconspicuous bracts upon the pedicel of each flower. The ordinary well-developed inflorescence of the majority of species of the genus produces four to ten flowers, but an exception is found in the case of *S. pauciflora* which normally develop but one flower for each cyme, although one to several abortive buds may appear.

The bracts usually directly subtend the flower, but in certain species, as in *S. eubracteata,* may appear about midway upon the pedicel. The character of the bract is a differentiating criterion between the genera *Tabernaemontana* and *Stemmadenia,* since in the former genus the bract always subtends the pedicel or aborts entirely.

Calyx.—The calyx consists of five imbricate lobes of unequal size, the three interior being somewhat larger, and usually more nearly colorless than the two smaller exterior lobes. Upon the interior of the calyx-tube, near the attachment to the disc, are borne several cycles of small fusiform glands, which may vary in approximate number from fifty to over one hundred. The unequal lobes of the calyx and the unusual number of the calycine glands are obvious distinguishing marks of the genus.

The relative length of the calyx-lobes and the general size of the calyx are of basic importance in the speciation of the genus, and form at once an evident, and it is believed a reliable and natural, taxonomic criterion. The lobes may vary from 2 cm. in some species to 1 mm. long in others, and are usually distinct for the various species.

Corolla.—The genus *Stemmadenia* is at once divisible into two subgenera largely upon the basis of the form of the corolla. The sections are also based upon this character. The corolla is salverform in the subgenus *Ochrodaphne*, and infundibuliform in the subgenus *Eustemmadenia.* The salverform corollas of *Ochrodaphne* are fairly regular, but the infundibuliform corollas of *Eustemmadenia* divide into two series, namely, that of the section *obovatae,* with a conical proper-throat and a spirally twisted tube, and that of the section *Galeottiae,* with a cylindrical proper-throat and a tube without spiral twisting. The relation of the proper-throat to the proper-tube of the infundibuliform corollas is again apparently a matter of taxonomic importance in the case of certain species, as is also the length of the limb.

Within the corolla-tube, above and opposite the attachment of the stamens, are five conspicuous appendiculate folds which vary considerably in length, but are constant for the genus.

The corollas are large and showy, and are either yellow or yellowish white in color. The five equal lobes of the limb are dextrorsely deflexed, especially in the subgenus *Ochrodaphne.*

Stamens.—The five stamens are wholly inserted, and are attached to the corolla-tube by short, thick, unguiculate filaments. The two sporangia comprising the anthers are elongate-fusiform in shape, and may be practically parallel, as in the subgenus *Ochrodaphne,* or obviously divergent at the base of the anther, as in the subgenus *Eustemmadenia.* The anthers are entirely fertile and unappendaged.

Pistil.—The pistil is typically bi-carpellate. The carpels are sessile and are separate except at the apices, which connive to form the filamentous style. Each carpel is uniloculate and contains many ovules upon a binate ventral placenta. The stigma is borne upon a fleshy terminal clavuncle.

Disc.—The disc proper is inconspicuous, shallow, and im-

mersed, but is surmounted by a ring of five conspicuous fleshy nectaries about the pistil, which, however, are actually coalesced into a more or less unified ring. The nectaries are partially adnate to the walls of the carpels, at least at the base. The nectaries appear of little taxonomic use.

Fruit.—The fruit consists of a pair of divaricate, leathery, glandular-punctate follicles containing many striate, albuminous, ecomose seeds immersed in an oily arilar pulp. The leathery pericarp eventually becomes coriaceous, and appears at that time to undergo a ventral dehiscence. The embryo is straight. It appears probable that were fruiting specimens of each species abundant peculiar diagnostic characters would be available based upon the general shape and size, form of glandulosity, etc. At present, however, the fruit of relatively few species is known, and in the following keys, the fruit is entirely omitted.

Systematic Position

Concerning the affinities of the genus *Stemmadenia*, Richard was much better orientated than Bentham. Bentham,[1] in describing the genus, wrote in part: "The size and form of the flowers in the above three species [*S. glabra*, *S. pubescens*, and *S. mollis*] are those of a *Cerbera* or a *Thevetia* from both of which, however, they differ in the calycine glands, and from the latter in the ovary; and in many points also there is a considerable degree of affinity with *Odontadenia*, but that genus again has not the remarkable calyx and glands of *Stemmadenia* . . ." Since superficially all large flowers resemble one another, Bentham was right in associating his new genus with *Cerbera* and *Thevetia*, although he does not mention the significant differences between those genera and *Stemmadenia*. However, in referring to an affinity with *Odontadenia* the fallibility of the obvious is well demonstrated, for *Stemmadenia*, with unappendaged anthers, non-connivent stamens, fleshy follicles, and ecomose seeds, is about as distantly related to *Odontadenia*, with appendaged anthers, connivent stamens, chartaceous follicles, and heavily comose seeds, as two genera in the same family

[1] Benth., *l. c.* 125. 1844.

could be. More recently Miers,[1] evidently deceived by the external similarity of the flowers of *Stemmadenia* to the showy flowers of the *Echitoideae,* pictured the stamens of *S. insignis* with conspicuous basal appendages.

Richard[2] displayed an understanding view of the morphology of Apocynaceous genera when, in describing *Odontostigma,* he remarked "Difiere del genero *Thevetia* sobre todo por su caliz, mas ancho y mas largo y por sus ovarios distintos, conteniendo cada uno gran numero de ovulos y no dos ovulos solamente como en el genero *Thevetia.*" Miers, in following Richard's carpological view of the subject, has justly associated *Stemmadenia* with *Tabernaemontana,* its nearest relative, but has evidently failed to make sufficiently clear the differences which exist between them.

In summing up the results of recent study, it is clear that *Stemmadenia,* by reason of its unappendaged anthers and non-connivent stamens, is a member of the subfamily Plumeroideae of Apocynaceae. Furthermore, by reason of its two carpels forming a divaricate fruit, it belongs to the tribe Plumereae. Finally, the fleshy follicles ally the genus immediately with the genera *Cerbera, Thevetia, Vallesia,* and *Tabernaemontana* in the subtribe *Tabernaemontaninae.*

From the genera *Cerbera, Thevetia,* and *Vallesia, Stemmadenia* differs, as Bentham and Richard have indicated, in the nature of the calycine glands, which are so conspicuously multiplied in *Stemmadenia,* in the calyx, which is conspicuously irregular in the latter genus and regular in *Cerbera* and *Thevetia* and *Vallesia,* and in the fruit, which is monospermous in the latter three genera and polyspermous in *Stemmadenia.* Finally, it is noteworthy that the carpels in *Cerbera* and *Thevetia* develop together, while those of *Stemmadenia* become widely divaricate, in which character it appears related to *Vallesia.*

From the genus *Vallesia, Stemmadenia* also differs in the corolla, which is much larger than in the former genus, and in the inflorescence, which is more reduced. The fleshy pericarp of *Vallesia,* also, is watery and evanescent, differing from the leathery persistent pericarp of *Stemmadenia.*

[1] Miers, *l. c. pl. 10B.* 1878.
[2] Richard, *l. c.* 1853.

The differences between *Tabernaemontana* and *Stemmadenia* have not always been easy to perceive. The most conspicuous difference is in the size of the flowers, which is much greater in the latter genus than in the former. However, technical characters are several and concise. The irregularity of the calyx of *Stemmadenia* again sets it apart from the regular calyx of *Tabernaemontana*. The interior of the corolla-tube in *Tabernaemontana* is naked, and contains appendiculate folds in *Stemmadenia*. The calycine glands of the former are uniseriate, while those of the latter are multiseriate. The nectaries of the former are completely coalesced and adnate to the carpels; the nectaries of the latter are only partially coalesced and are scarcely adnate to the carpels. The filaments of the former are straight, while those of the latter are unguiculate. Also it is believed that the fruit of *Stemmadenia*, which is much larger than that of *Tabernaemontana*, is eventually dehiscent along a ventral suture, while that of the latter genus is always indehiscent. The corolla of *Stemmadenia* is infundibuliform, or, if salverform, the tube is spirally twisted and the calyx is immediately subtended by three bracts, while in *Tabernaemontana* the corolla is always salverform, although the tube is not spirally twisted and bracts are limited to one or two, which subtend the pedicel rather than the calyx itself or are lacking.

Relationships within the Genus

As has already been explained, the genus *Stemmadenia* is readily divisible into two subgenera. The subgenus *Eustemmadenia* comprises plants with infundibuliform corollas, the lobes of which are slightly deflexed dextrorsely. The calyx squamellae are in several series. The sporangia of the anthers are divergent at the base.

The species of the subgenus *Ochrodaphne* possess salverform corollas with lobes which are conspicuously deflexed dextrorsely, and auriculate, giving the flower a striking turbinate appearance. The calyx squamellae are fewer than those of *Eustemmadenia* and are usually in only two or three series. The sporangia of the anthers are nearly parallel to the base.

The pistil of *Ochrodaphne*, also, represents a condition much

nearer coalescence of the carpels than that of *Eustemmadenia.* The carpels of *Eustemmadenia* are prolonged into two distinct stylopodium-like beaks before they finally unite into a common style bearing the stigmatic clavuncle. On the other hand, the

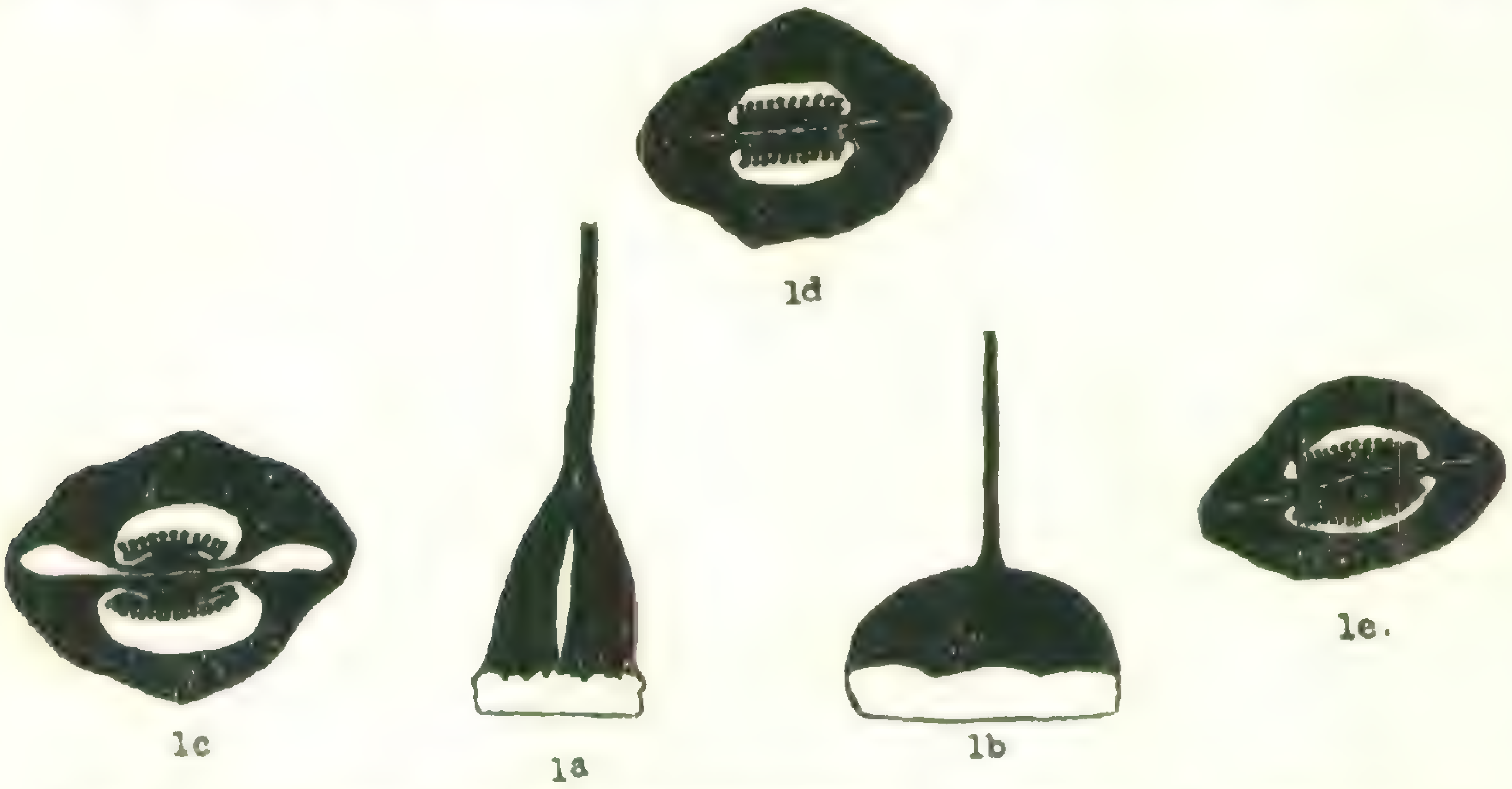


Fig. 1. Carpellary diagrams of *Stemmadenia.* 1a, pistil of *S. tomentosa* var. *Palmeri;* 1b, pistil of *S. grandiflora;* 1c, cross-section of ovary of *S. tomentosa* var. *Palmeri;* 1d, cross-section of ovary of *S. Galeottiana;* 1e, cross-section of ovary of *S. grandiflora.*

style of *Ochrodaphne* arises directly from the summit of the truncate carpels. Diagrams of the pistils of *Eustemmadenia* and *Ochrodaphne* are found in fig. 1, which also diagrams a difference in placentation occurring between the two subgenera.

Eustemmadenia appears to be the more primitive of the subgenera and *Ochrodaphne* the more advanced because of the form of the corollas and pistils of those groups, and also by reason of the reduced calyx-squamellae of the latter. In a future paper reasons for assuming the floral squamellae frequently occurring in the Apocynaceae as staminal vestiges will be fully discussed, and until then the reasons for regarding the reduction of squamellae as a modified rather than a primitive state must remain implied.

For morphological reasons which have already been advanced, *Stemmadenia* is apparently more primitive than its closest neighboring genus, *Tabernaemontana,* and should therefore logically be placed after that genus in a phylogenetic synopsis of the family Apocynaceae. At present, in the system of K. Schu-

mann in Engler and Prantl's 'Naturlichen Pflanzenfamilien,' this order is reversed. This latter order is also found in the 'Genera Phanerogamarum' of Dalla Torre and Harms. The logic of viewing *Stemmadenia* as more primitive rather than more advanced than *Tabernaemontana* is perceived when the genus is split into the two subgenera, *Eustemmadenia* and *Ochrodaphne,* indicating an advance from a simple corolla and numerous squamellae to a more highly modified corolla and reduced squamellae, including an advance in the coalescence of the carpels, tendencies finally developing a climax in the morphology of the genus *Tabernaemontana.*

The species within the group *Ochrodaphne* are homogeneous and not divisible into subgroups, but the species of *Eustemmadenia* are clearly divisible into two sections, illustrating an approach from the infundibuliform corolla characteristic of the subgenus to the salverform corolla of *Ochrodaphne.* Of these, the *obovatae* possess a typically infundibuliform corolla with a nearly conical proper-throat and a dextrorsely twisted tube, while the *Galeottiae* possess a modified form of infundibuliform corolla with a long cylindrical proper-throat, and a tube which is without dextrorse spiral twisting. Apparently the only other morphological difference which accompanies the corollar characters of these sections is the amount of space left between the carpels as an index of the degree to which carpellar fusion has progressed. Figs. 1c and 1d illustrate diagrammatically cross-sections of the pistils of *S. tomentosa* var. *Palmeri* and *S. Galeottiana,* representatives respectively of the sections *obovatae* and *Galeottiae.* It is easily perceived that the carpels of the latter are the more nearly coalesced, which corroborates the judgment of it as the more advanced, phylogenetically. The carpels of the subgenus *Ochrodaphne,* as fig. 1e testifies, are at about the same stage of coalescence as those of the *Galeottiae* section of *Eustemmadenia.*

Geographical Distribution

The genus *Stemmadenia* is confined apparently to the tropical regions of continental America, lying between the Equator and the Tropic of Cancer roughly, although it also occurs slightly more to the north of those arbitrary bounds as far as southern

Chihuahua in Mexico, and doubtless also farther to the south, especially in Ecuador.

The species of the genus are frequenters of sub-Cordilleran underbrush, and range in height from two to twelve meters for mature specimens. The fruit is said by Miers to constitute a favorite food for the larger birds of the region, and seeds are probably distributed by means of those agents.

As fig. 2 indicates, the subgenus *Eustemmadenia* and the subgenus *Ochrodaphne* coincide in their ranges in Central America, but have distinctive ranges, *Eustemmadenia* towards the North, and *Ochrodaphne* towards the South. However, *S. obovata* var. *mollis*, one of the most widespread and common representatives of *Eustemmadenia* sect. *obovatae,* has twice been collected about Guayaquil, Ecuador, and once near Yungas, Bolivia, imparting a most singular appearance to a map of the distribution of the genus. The disrupted nature of the distribution of the subgenus *Eustemmadenia* thus disclosed urges a consideration of it as a relict group; thus as in all probability the more primitive of the subgenera, and the section *obovatae* as the ancestor of the entire group, even as a study of the morphology alone indicated.

Although Richard, in describing *Odontostigma Galeottiana,* stated that the specimens were from the environs of Havana, Cuba, and although one would naturally expect to find representatives of a genus so frequent naturally in Central America in the Antilles, no evidence of the presence of the genus in Cuba or the other Caribbean Islands has been found, either in herbaria or in published floras of the region. It appears probable that Galeotti's specimen from which Richard drew his description was in reality collected in Mexico, rather than in Cuba, as was understood by Richard.

ABBREVIATIONS

In citing specimens, the following abbreviations for herbaria have been employed: G = Gray Herbarium of Harvard University; NY = Herbarium of the New York Botanical Garden; US = United States National Herbarium; ANSP = Academy of Natural Sciences of Philadelphia; F = Herbarium of the Field

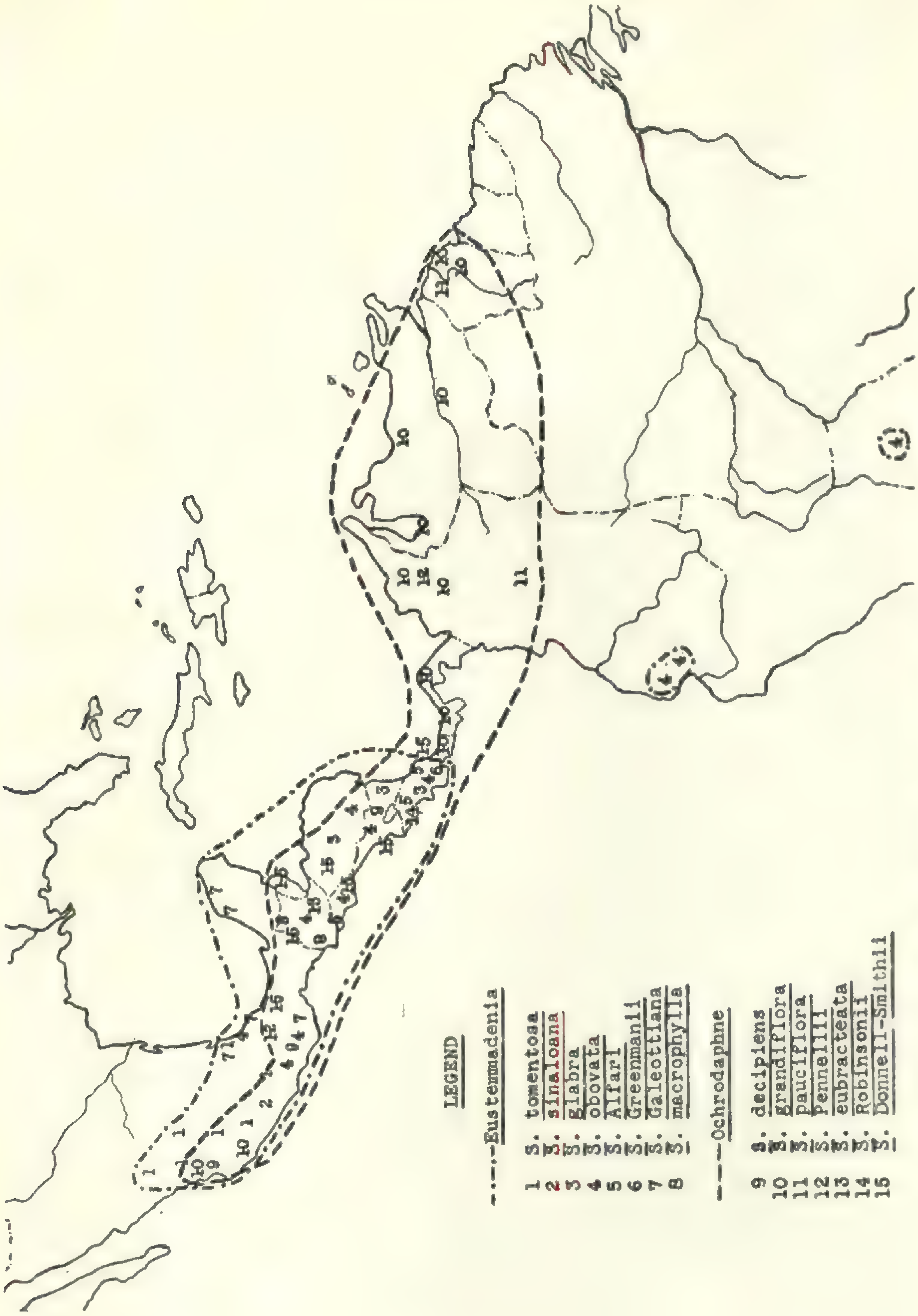


Fig. 2.—Showing distribution of species of *Stemmadenia*

Museum of Natural History; MBG = Herbarium of the Missouri Botanical Garden.

TAXONOMY

Stemmadenia Benth. Bot. Voy. Sulph. 124. *t. 44.* 1844; Lindl. Veg. Kingd. 601. 1847; Walp. Rep. 468. 1847; Pfeif. Nom. Bot. **2**²: 1270. 1874; Benth. & Hook. Gen. Pl. **2**: 707. 1876; Miers, Apoc. S. Am. 74. 1878; Hemsl. Biol. Cent.-Am. Bot. **2**: 310. 1881; Durand, Ind. Gen. Phan. n. 4615. 1888; Baill. Hist. Pl. **10**: 196. 1891; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**²: 148. 1895; Standl. Contr. U. S. Nat. Herb. **23**: 1155. 1924.

Odontostigma A. Rich. (non Zoll. & Mor.) Fl. Cub. Fanerog. **2**: 86. 1853.

Stemmaderia B. D. Jackson, Ind. Kew. **2**: 331. 1894. err. typ.

Lactescent shrubs or small trees 2–15 m. tall. Leaves entire, opposite, glabrous or pubescent, petiolate, the sheaths of the petioles meeting in a shallow ring about the stem and sheltering in the crux many small fusiform glands. Inflorescence a terminal reduced raceme of several flowers. Corolla large, infundibuliform or salverform, white or yellow, the limb of 5 equal lobes dextrorsely reflexed and occasionally auriculate, bearing 5 linear interior appendiculate folds opposite and slightly above the attachment of the stamens. Calyx 5-parted, the lobes imbricate, unequal, usually 3 larger interior and 2 smaller exterior, bearing several cycles of small fusiform glands within and near the attachment of the disc. Stamens 5, included, attached to the corolla at the summit of the proper-tube, alternate with the corolla-lobes; filaments very short and thick, unguiculate at the attachment to the anthers; anthers of 2 elongate unappendaged sporangia. Carpels 2, sessile, unilocular, bearing many ovules upon a lateral binate ventral placenta, produced apically into a long filiform style; stigma terminal, borne upon a fleshy truncate clavuncle. Disc proper shallow, immersed, entire; nectaries fleshy, coalesced into a more or less irregular ring about, and slightly adnate to, the carpels. Fruit a pair of divaricate, leathery, glandular-punctate follicles containing many striate, albuminous, ecomose seeds immersed in an oily arilar pulp; embryo straight.

Type species: *S. glabra* Benth. Bot. Voy. Sulph. 124. *t. 44.* 1844.

SYNOPSIS OF THE SUBGENERA AND SECTIONS

KEY TO THE SUBGENERA

Corolla infundibuliform, the lobes dextrorsely reflexed, but only slightly auriculate; bracts immediately subtending the calyx. ....Subgen. I. EUSTEMMADENIA

Corolla salverform, the lobes dextrorsely reflexed and very strongly auriculate; bracts placed about midway upon the pedicels. .Subgen. II. OCHRODAPHNE

SUBGENUS I. EUSTEMMADENIA Woodson

Subgenus I. EUSTEMMADENIA Woodson, n. subgen.

Corolla infundibuliform, the lobes dextrorsely reflexed and very slightly auriculate; calyx-squamellae in several series of different lengths; sporangia of the anthers divergent at the base; rim of the coalesced nectaries irregularly folded and lobed; corollar appendages relatively long, 1.5–2.0 cm. long; bracts immediately subtending the calyx.

Section 1. OBOVATAE Woodson. Proper-throat of the corolla conical, about as long as broad.

KEY TO THE SPECIES

a. Calyx relatively short, 1–5 mm. long.
  b. Calyx-lobes oblong to ovate, acute at the apex, 3–5 mm. long.
    c. Under-surface of leaves persistently and uniformly tomentose. ....*1. S. tomentosa*
    cc. Under-surface of leaves slightly barbate in the axils of the midvein, becoming glabrous or glabrate....*1a. S. tomentosa* var. *Palmeri*
  bb. Calyx-lobes subreniform, rounded at the apex, 1–2 mm. long. . .*2. S. sinaloana*
aa. Calyx relatively long, 1.5–3 cm. long.
  b. Proper-tube about as long as the calyx; inflorescence glabrous. . .*3. S. glabra*
  bb. Proper-tube much surpassing the calyx; inflorescence pubescent.
    c. Upper-surface of leaves glabrate.........................*4. S. obovata*
    cc. Upper-surface of leaves persistently pubescent. . .*4a. S. obovata* var. *mollis*

1. Stemmadenia tomentosa Greenm. Proc. Am. Acad. 35: 310. 1900; Standl. Contr. U. S. Nat. Herb. 23: 1156. 1924.

Shrubs or small trees, 2–12 m. tall; leaves 8–15 cm. long, 5–7 cm. broad, glabrous or glabrate above, tomentose beneath, petioles 4–8 mm. long; inflorescence 2–5-flowered; corolla yellow, the proper-tube 2–2.5 cm. long, the proper-throat conical,

2–3 cm. long, 1.5–2 cm. broad at the orifice, the limb 2–3 cm. broad; calyx-lobes 4–5 mm. long, the segments oblong to ovate, acute at the apex, somewhat imbricate, both the larger and the smaller yellowish; follicles 4–4.5 cm. long, 3–3.5 cm. broad, acute at the apex.

Distribution: waste-lands, central and southern Mexico.

Specimens examined:

Mexico:

Vera Cruz: San Juan, 1889, *Heilprin & Baker* (ANSP).

Jalisco: lava beds near Zapotlan, May 19, 1893, *Pringle 4370* (G type, NY, US, MBG).

Sinaloa: Sinaloa, April 2, 1910, *Rose, Standley & Russell 13874* (US).

1a. Var. **Palmeri** (Rose) Woodson, n. comb.

Stemmadenia Palmeri "Kosc." ex Urbina, Pl. Mex. 214. 1897, *nomen*.

Stemmadenia Palmeri Rose ex Greenm. Proc. Am. Acad. **35**: 311. 1900.

"*Stemmadenia Palmeri* Rose & Standl." in Standl. Contr. U. S. Nat. Herb. **23**: 1156. 1924.

Leaves glabrous or glabrate above, beneath barbate in the axils of the midvein, or glabrate; calyx-lobes 3–5 mm. long, greenish.

Distribution: waste-land, and hedgerows, general over central and southern Mexico.

Specimens examined:

Mexico:

Chihuahua: Tierras Verdes, May, 1891, *Hartmann 534* (G); southwestern Chihuahua, Aug.–Nov. 1885, *E. Palmer M* (G, US); Batopillas, April, 1892, *Hartmann 1032* (G).

Sinaloa: Ymala, Aug. 16–25, 1891, *E. Palmer 1470* (US type); Mazotlan, April 5, 1910, *Rose, Standley & Russell 14064* (US); vicinity of Rosario, April 14, 1910, *Rose, Standley & Russell 14544* (US); San Ignacio, June 19, 1918, *Montes & Salazar 405* (US); Guadalcupe, April 18, 1910, *Rose, Standley & Russell 14675* (US); La Cruz, 1921, *Ortega 4175* (US); between Rosario and Concepcion, July 27, 1897, *Rose 3260* (US); San

Ignacio, March 12, 1918, *Montes & Salazar 268* (US); Rosario, July 8, 1897, *Rose 1573* (US); Colomas, July 16, 1897, *Rose 1688* (US).

Jalisco: Baranca, near Guadalajara, June, 1886, *E. Palmer 132* (G, US); Chiquilistlan, May 15, 1892, *Jones 335* (MBG, US); Tequila, July 5–6, 1899, *Rose & Hough 4777* (US); Baranca, near Guadalajara, May 28, 1891, *Pringle 5151* (G); vicinity of Colima, April 5, 1897, *Seler 3436* (G); Baranca of Guadalajara, alt. 4000 ft., June 10, 1898, *Pringle 6872* (G, NY, F, ANSP, US, MBG); Guadalajara, June 25, 1892, *Pringle 5363* (G); San Sebastien, Jan. 15, 1927, *Mexia 1490* (US); Bolanos Aug. 10–19, 1897, *Rose 2888* (US).

Durango: Chocala, March 7, 1899, *Goldman 358* (US).

Morelos: Cuernavaca, May 11, 1898, *Pringle 6847* (US).

Nayarit: Ojos de Agua, near Ixtlan, Sept. 23, 1926, *Mexia 733* (US).

Popular names of this variety are "Berrarco," "Berraco ó Tapaco," and the gum of the fruit is said to be used like chicle (*Montes & Salazar 405*, US).

The embarrassment of monographers who find themselves forced to regard as "typical" an anomalous form of a species because of priority in publication over a more common variety is illustrated in a peculiar fashion by *Stemmadenia tomentosa* Greenm. and its var. *Palmeri*. As early as 1891 the herbarium name "*Stemmadenia Palmeri* Rose" was distributed with specimens of the glabrescent or barbate variety of the former species. The name did not appear in publication, however, until 1893, when Urbina, in compiling his 'Catalogue of Mexican Plants,' happened upon specimens of the genus bearing the inscription of *S. Palmeri* Rose in a rather poor script, and erroneously published the name for the first time as a *nomen nudum*. Urbina mistook the name of Dr. Rose for an abbreviation, and gave the author as "Kosc." It is indeed fortunate that a description was not included under that authorship.

In 1900 Dr. Greenman published *Stemmadenia tomentosa*, and in so doing spoke of the characteristics of *S. Palmeri* Rose, which he evidently assumed to be a correctly published name. It was not until 1924 that *Stemmadenia Palmeri* was published

by Rose in Standley's 'Trees and Shrubs of Mexico.' The legal place of publication of the species must evidently be regarded as ex Greenman, Proc. Am. Acad. 35: 311. 1900.

2. **Stemmadenia sinaloana** Woodson, n. sp.[1] Pl. 48, fig. 1.

Shrubs or small trees; leaves 8–12 cm. long, 5–6 cm. broad, glabrous, or very slightly puberulent upon the lower surface, petiolate, the petioles 7–10 mm. long; inflorescence 1–4-flowered; corolla yellow, the proper-tube 1.5–2 cm. long, the proper-throat conical, about 1.5 cm. long, about 1.5 cm. broad at the orifice, the limb 1.5–2 cm. long; calyx about one-sixteenth the length of the proper tube, the segments ovate-reniform, 1.2 mm. long, about 4 mm. broad, obtuse at the apex, or completely rounded, scarcely imbricated, unequal, greenish; follicles unknown.

Distribution: known only from the type locality in Sinaloa.

Specimens examined:

MEXICO:

SINALOA: Rosario, Jan. 1895, *Lamb 467* (G TYPE).

S. sinaloana is especially noteworthy in the genus *Stemmadenia* by reason of its peculiarly reduced calyx. In that respect it is closest related to *S. tomentosa* Greenm., from which it differs in having a calyx less than one-half as large (1–2 mm. long), and in having the calyx-lobes subreniform and rounded at the apex instead of oblong and ovate with acute or acuminate apex as in the latter species.

3. **Stemmadenia glabra** Benth. Bot. Voy. Sulph. 124. *t. 44.* 1844; Hemsl. Biol. Cent.-Am. Bot. 2: 310. 1881; Miers, Apoc. S. Am. 74. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4^2: 149. 1895; Standl. Contr. U. S. Nat. Herb. 23: 1156. 1925; Standl. & Calderón, Lista Prélim. Pl. Sal. 174. 1925. Pl. 47, fig. 1.

Shrubs or small trees, 2–10 m. tall; leaves 14–20 cm. long, 7–8 cm. broad, glabrous, petiolate, petioles 5–10 mm. long;

[1] Stemmadenia sinaloana sp. nov., arborea glabra vel subpuberulenta; foliis oblongo-lanceolatis 8–12 cm. longis 5–6 cm. latis; petiolis 7–10 mm. longis; corollae tubo conico-infundibuliformo 3–3.4 cm. longo, lobis ca. 1.5 cm. longis; calycis lobis parvis ovato-reniformibus inaequalibus ca. 2 mm. longis ca. 4 mm. latis obtusis, viridibus.—Sinaloa, Rosario, Jan. 1895, *F. H. Lamb 467* (Gray Herb., TYPE).

inflorescence 1–4-flowered; corolla deep yellow, the proper-tube 2–2.5 cm. long, the proper-throat conical, about 2 cm. long, 2–2.5 cm. broad at the orifice, the limb 2.5–3 cm. long; calyx about equalling the length of the proper tube, the segments 1.5–2.5 cm. long, .8–1.0 cm. broad, strongly imbricate in two unequal series, the larger yellow, the smaller greenish yellow; follicles about 5 cm. long, 3–3.5 cm. broad.

Distribution: tropical forests and thickets, Central America. Reported also from Mexico.

Specimens examined:

COSTA RICA: between San Pedro de Montes de Oca and Curridabat, Dept. San José, Feb. 2, 1924, *Standley 32793* (US); Cartago, Feb. 1924, *Standley 35459* (US).

HONDURAS: Amapala, Isla de Tigre, Feb. 14, 1922, *Standley 20713* (US).

EL SALVADOR: vicinity of La Unión, Dept. La Unión, alt. 150 m., Feb. 13–21, 1922, *Standley 20686* (G, NY, US); Laguna de Magugüe, Dept. La Unión, alt. 60 m., Feb. 18, 1922, *Standley 20943* (G, NY, US); La Unión, Sept. 21, 1860, *Sutton-Hayes* (G).

NICARAGUA: southwestern slopes of Santiago Volcano, near Masaya, alt. 300–480 m., July 5, 1923, *Maxon 7647* (G, US); Ometepe Island, Jan. 1893, *C. L. Smith* (G); Managua, shores of Lake Managua, June 24, 1923, *Maxon, Harvey & Valentine 7270* (US); Managua, vicinity, June 30, 1923, *Maxon, Harvey & Valentine 7539* (US); Laguna de Masaya, July 6, 1923, *Maxon 7727* (US).

Dr. Sutton Hayes remarks (*Sutton-Hayes*, G) that the popular name of this species in El Salvador is "Cajon del Mico." According to Standley (*Standley 32793*, US), the popular name in Costa Rica is "huevos de Caballo," or "Girijarro," and the sap is used for corns and tooth-ache.

4. Stemmadenia obovata (Hook. & Arn.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4^2: 149. 1895.

Bignonia (?) obovata Hook. & Arn. Bot. Beech. Voy. 439. 1841.

Stemmadenia pubescens Benth. Bot. Voy. Sulph. 125. 1844;

Miers, Apoc. S. Am. 74. 1878; Hemsl. Biol. Cent.-Am. Bot. **2**: 310. 1881.

Shrubs or small trees, 2–15 m. tall; leaves 10–20 cm. long, 7–10 cm. broad, pubescent, or glabrate above, petiolate, petioles 5–8 mm. long; inflorescence 1–6-flowered; corolla deep yellow, the proper-tube 1.5–2.5 cm. long, the proper-throat 1.5–3 cm. long, 2–2.5 cm. broad at the orifice, the limb 1.5–2.5 cm. long; calyx much surpassed by the length of the proper-tube, the segments 1.5–2 cm. long, .8–1.0 cm. broad, strongly imbricated in two unequal series, both series yellowish; follicles 4–4.5 cm. long, 3–3.5 cm. broad, acute at the apex.

Distribution: tropical forests and thickets, southern Mexico and Central America.

Specimens examined:

MEXICO:

GUERRERO: El Correjo, alt. 900 m., May 18, 1899, *Langlassé 1029* (G).

COSTA RICA: Salinas, July, 1890, *Pittier 1177* (US).

NICARAGUA: Managua, vicinity, June 30, 1923, *Maxon, Harvey & Valentine 7542* (US); La Paz, Dept. Leon, Jan. 31, 1903, *Baker 2270* (G, US); Managua, June 30, 1926, *Chaves 215* (US).

EL SALVADOR: near La Cebadilla, 1922, *Calderón 1230* (G); Laguna de Olomega, Dept. San Miguel, alt. 75 m., Feb. 20, 1922, *Standley 21034* (G).

4a. Var. mollis (Benth.) Woodson, n. comb.

Stemmadenia mollis Benth. Bot. Voy. Sulph. 125. 1844; Hemsl. Biol. Cent.-Am. Bot. **2**: 310. 1881; Miers, Apoc. S. Am. 75. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**^{2}: 149. 1895; Urbina, Pl. Mex. 214. 1897; Donn.-Sm. Enum. Pl. Guat. **4**: 105. 1895; Areschoug, Pl. ca. Guayaquil Coll. 127. 1910; Standl. Contr. U. S. Nat. Herb. **23**: 1156. 1924; Standl. & Calderón, Lista Prélim. Pl. Sal. 174. 1925.

Stemmadenia calycina Brandg. Univ. Cal. Publ. Bot. **10**: 188. 1922.

Upper surface of leaves persistently tomentose.

Distribution: tropical forests and hedgerows, southern Mexico, northern Central America, and northwest-central South America.

Specimens examined:

MEXICO:

VERA CRUZ: Baños del Carrizal, Aug. 1912, *Purpus 6230* (G, NY, US, MBG); San Francisco, May, 1894, *C. L. Smith 1339–1374* (G); Remulatero, April, 1922, *Purpus 8771* (G, NY, US, MBG).

GUERRERO: Iguala, Aug. 1905, *Rose, Painter & Rose 9274* (MBG, NY, US); El Correjo, May 18, 1899, *Langlassé 1029* (US).

OAXACA: Camino de Tonomeca, May 7, 1917, *Conzatti & Reko 3258* (US, MBG).

CHIAPAS: Petapa, May 29, 1904, *Goldman 1027* (US).

COSTA RICA: Salinas, July, 1890, *Pittier 2908* (US); Nicoya, April, 1900, *Tonduz 13900* (G, NY, US); Liberia, Dept. Guanacaste, April, 1893, *Shannon 5042* (US); Las Huacas, Nicoya Peninsula, May 24, 1903, *Cook & Doyle 723* (US).

EL SALVADOR: Sonsonate, Dept. Sonsonate, alt. 220–300 m., March 18–27, 1922, *Standley 22372* (G, NY, US); Laguna de Olomega, Dept. San Miguel, Feb. 20, 1922, *Standley 21034* (US); La Cebadilla, Dept. San Salvador, 1922, *Calderon 1230* (US); between San Martin and Laguna de Ilopanga, Dept. San Salvador, April 1, 1922, *Standley 22539* (US).

NICARAGUA: Momotombo, May 27, 1895, *C. L. Smith 126* (G, NY); Los Braziles, Jan. 28, 1928, *Mell 28* (NY); south of Managua, March 3, 1922, *Greenman & Greenman 5713* (MBG).

GUATEMALA: Fiscal, alt. 3700 ft., May 31, 1909, *Deam 6070* (G, US); Agua Caliente, March 28, 1922, *Greenman & Greenman 5920* (MBG); Barranquillo, Dept. El Progreso, May 21, 1920, *Popenoe 977* (US); between Chiquín and Crapeche Grande, Dept. Guatemala, March 19, 1905, *Pittier 133* (US); El Rancho, Dept. Jalapa, April 4, 1905, *Maxon & Hay 3766* (US); Dept. Jalapa, March 10, 1905, *Kellerman 4511* (US).

ECUADOR: Guayaquil, Feb. 1885, *Rusby 931* (NY); hillsides near Guayaquil, Sept.–Oct. 1925, *Mille 59* (NY); Durán, Nov. 5–8, 1918, *Rose & Rose 23612* (NY).

BOLIVIA: near Yungas, alt. 4000 ft., 1885, *Rusby 1163* (NY).

Section 2. GALEOTTIAE Woodson. Proper-throat of the corolla cylindrical, much longer than broad.

Key to the Species

a. Proper-tube about equalling the length of the proper-throat; corolla-tube, *sensu-latiore*, 3–3.5 cm. long.
  b. Calyx-lobes 1.5–2 mm. long; corolla-limb 5–8 mm. broad.....*5. S. Alfari*
  bb. Calyx-lobes 5–7 mm. long; corolla-limb 10–15 mm. broad..*6. S. Greenmanii*
aa. Proper-tube much surpassed by the length of the proper-throat; corolla-tube, *sensu-latiore*, 4.5–6 cm. long.
  b. Calyx 1–1.5 cm. long, the lobes distinctly imbricated.....*7. S. Galeottiana*
  bb. Calyx 4–5 mm. long, the lobes scarcely imbricated.......*8. S. macrophylla*

5. **Stemmadenia Alfari** (Donn.-Sm.) Woodson, n. comb.

Tabernaemontana Alfari Donn.-Sm. Bot. Gaz **24**: 396. 1897.

Small tree 3–4 m. tall; leaves 7–11 cm. long, 3.5–5 cm. broad, glabrous, acuminate, subspathulate, petiolate, petioles 1–1.5 cm. long; inflorescence 1–3-flowered; corolla infundibuliform or occasionally subinfundibuliform, yellow or yellowish white, the tube, *sensu-latiore*, 3–3.5 cm. long, the limb 1–1.5 cm. broad; calyx-lobes 1.5–2 mm. long, 1.5–2 mm. broad, scarcely imbricated in two series, both the inner and the outer yellowish; follicles unknown.

Distribution: hedgerows and waste-lands, Costa Rica.

Specimens examined:

Costa Rica: San Pedro, near San Ramón, hedgerows, alt. 1300 m., April 13, 1913, *Tonduz 17653* (F); Limoncito and Vuelta, alt. 1100 m., March, 1897, *Pittier 11094* (US type).

6. **Stemmadenia Greenmanii** Woodson, n. sp.[1] Pl. 48, fig. 2.

Shrubs or small trees 1–6 m. tall; leaves 8–12 cm. long, 4–5 cm. broad, glabrous, petiolate, petioles 5–8 mm. long; inflorescence 2–5-flowered; corolla yellowish white, the proper-tube about 1.5 cm. long, the proper-throat cylindrical, about 2.0 cm. long, about .8 cm. broad at the orifice, the limb 1–1.5 cm. broad; calyx about one-third the length of the proper-tube, the segments .5–.7 cm. long, .3–.4 cm. broad, strongly imbricated in two unequal series, both series yellowish; immature specimens oblong-lanceolate, acute at the apex.

[1] **Stemmadenia Greenmanii** sp. nov., arborea glabra; foliis oblongo-lanceolatis 8–12 cm. longis 4–5 cm. latis; petiolis 5–8 mm. longis; corollae tubo cylindrico-infundibuliformo 3–5 cm. longo, lobis 1–1.5 cm. longis; lobis calycis ovatis inaequalibus ca. .5 cm. longis 3–4 mm. latis flavis; folliculis oblongo-lanceolatis acutibusque.—Costa Rica, San Ramon, June 4, 1901, *Brenes 14275* (Gray Herb., type).

Distribution: tropical forests and thickets, Costa Rica.

Specimens examined:

Costa Rica: San Ramón, alt. 1100 m., May 29, 1901, *Brenes 14275* (G type); San Ramón, June 4, 1901, *Brenes 14278* (G).

This species is evidently very local, but is very distinct. The nearest related species is undoubtedly *S. Alfari*, from which, however, it differs radically in the size of the calyx and all the floral parts. The species is dedicated to Dr. J. M. Greenman, by all odds the most discriminating of recent students of the group.

7. **Stemmadenia Galeottiana** (A. Rich.) Miers, Apoc. S. Am. 76. 1878. Pl. 47, figs. 2–3.

Odontostigma Galeottiana A. Rich. in Sagra, Hist. Cub. **11**: 868. *t. 60* (Fl. Cub. Fanerog. **2**: 86). 1853; Walp. Ann. **5**: 477. 1858.

Echites bignoniaeflora Schl. Linnaea **26**: 372. 1853.

Stemmadenia bignoniaeflora (Schl.) Miers, Apoc. S. Am. 76. 1878; Donn.-Sm. Enum. Pl. Guat. **5**: 51. 1899; Standl. Contr. U. S. Nat. Herb. **23**: 1156. 1924.

Stemmadenia insignis Miers, Apoc. S. Am. 76. *t. 10B.* 1878; Hemsl. Biol. Cent.-Am. Bot. **2**: 310. 1881; Standl. Contr. U. S. Nat. Herb. **23**: 1156. 1924.

Tabernaemontana laurifolia Schott (non L., nec Ker, neque Blanco) ex Miers Apoc. S. Am. 76. 1878 *nomen.*

Stemmadenia bella Miers, Apoc. S. Am. 77. 1878; Donn.-Sm. Enum. Pl. Guat. **5**: 51. 1899; Standl. Contr. U. S. Nat. Herb. **23**: 1156. 1924.

Stemmaderia Galeottianum B. D. Jackson, Ind. Kew. **2**: 331. 1844, err. typ.

Shrubs, 1–3 m. tall; leaves 9–12 cm. long, 4–5 cm. broad, glabrous or slightly puberulent upon the lower surface, petiolate, petioles 8–11 mm. long; inflorescence 1–4-flowered; corolla yellow, the proper-throat 4–5 cm. long, 1.0–1.3 cm. broad at the orifice, the proper-tube 8–10 mm. long, the limb 2.5–3 cm. long; calyx segments 10–14 mm. long, 4–7 mm. broad, strongly imbricated in two unequal series; follicles 2–2.5 cm. long, 1.5–1.7 cm. broad.

Distribution: tropical forests of southern Mexico and Costa Rica.

Specimens examined:

MEXICO:

VERA CRUZ: Teocelo, May 8, 1901, *Goldman 575* (US); Zacuapan, March, 1917, *Purpus 7740* (G, NY, US, MBG); Orizaba, March 23, 1867, *Bilimek 269* (G); Orizaba, date lacking, *Botteri 988* (G); Textolo, alt. 3500 ft., April 26, 1899, *Pringle 8103* (G, NY, ANSP, US, F, MBG); Orizaba, April, 1866, *Bourgeau 2440* (G, US).

OAXACA: exact locality lacking, 1841, *Galeotti 1605* (NY CO-TYPE?); Sontecomopan, *Galeotti 1599* (US).

YUCATAN: Merida, April 14, 1887, *Millspaugh 27* (F); Izamal, cultivated for its flowers, date lacking, *Gaumer 23204* (F); Merida, Quinta del Obispo, March 18, 1865, *Schott 430* (US, F).

Since *Odontostigma Galeottiana* A. Rich. and *Echites bignoniaeflora* Schl. were both published in 1853 at unknown months, according to the fly-leaves of the journals in which they appeared, it was perplexing whether to conserve *Stemmadenia Galeottiana* or *S. bignoniaeflora*. However, on the fly-leaf of Asa Gray's copy of 'Linnaea' **26**, in which *E. bignoniaeflora* was published, appears the note in Dr. Gray's handwriting that the publication did not actually leave the press until August, 1854. In the absence of contradiction, then, it is assumed that Richard's species appeared in 1853, and is therefore considered to have priority.

8. **Stemmadenia macrophylla** Greenm. Proc. Am. Acad. **35**: 310. 1900; Donn.-Sm. Enum. Pl. Guat. **6**: 83. 1903.

Shrubs or small trees; leaves 15–20 cm. long, 5–7 cm. broad, glabrous, petiolate, petioles 1.5–2 cm. long; inflorescence 1–4-flowered; corolla yellow, the proper-throat cylindrical, 2.5–3 cm. long, .8–1.2 cm. broad, the proper-tube 1.5–2 cm. long, the limb 2.5–3 cm. broad; calyx about one-half the length of the proper-tube, the segments 4–6 mm. long, 3–4 mm. broad, scarcely imbricated in two unequal series, both series yellowish; follicles unknown.

Distribution: tropical thickets of Guatemala.

Specimens examined:

GUATEMALA: Pansamalá, Dept. Alta Verapaz, alt. 3800 ft., Jan. 1886, *Tuerckheim 981* (G TYPE, NY, US, MBG); Coban, Dept. Alta Verapaz, April, 1889, *Donnell-Smith 1800* (US); San Carlos Miramar, March 19, 1921, 750 m., *Tonduz & Rojas 147* (MBG).

SUBGENUS II. OCHRODAPHNE Woodson

Subgenus I. OCHRODAPHNE Woodson, n. subgen.

Corolla salverform, the lobes dextrorsely reflexed and strongly auriculate; calyx-squamellae in two or three series of nearly uniform length; sporangia of the anthers nearly parallel to the base; rim of the coalesced nectaries nearly smooth; corollar appendages relatively short, 5–7 mm. long; bracts placed midway upon the pedicels. Name coined from ὠχρὸς, yellow, and δάφνη, laurel, from the popular name of *Stemmadenia grandiflora* (Jacq.) Miers, "Yellow Laurel."

KEY TO THE SPECIES

a. Calyx less than one-half the length of the corolla-tube.
 b. Bracts scarious; leaves ovate to ovate-oblong.
  c. Inner series of calyx-lobes only slightly longer than the outer; leaves glabrous throughout, glaucous beneath.
   d. Inflorescence several- or many-flowered; corolla-limb as broad as the length of the tube.
    e. Calyx-lobes 4–6 mm. long, yellowish, appressed; leaves ovate .... *9. decipiens*
    ee. Calyx-lobes 10–15 mm. long, green, spreading; leaves ovate-oblong .... *10. S. grandiflora*
   dd. Inflorescence 1-flowered by abortion; corolla-limb about one-half as broad as the length of the tube .. *11. S. pauciflora*
  cc. Inner series of calyx-lobes about twice as long as the outer; leaves finely rufose-puberulent beneath .... *12. S. Pennellii*
 bb. Bracts foliaceous; leaves lanceolate .... *13. S. eubracteata*
aa. Calyx equalling or nearly equalling the length of the corolla-tube.
 b. Calyx-lobes linear-lanceolate; leaves oblong-lanceolate, glabrous throughout .... *14. S. Robinsonii*
 bb. Calyx-lobes ovate; leaves spatulate, glabrous above, the under-surface conspicuously barbate in the axils of the midvein. .... *15. S. Donnell-Smithii*

9. Stemmadenia decipiens Woodson, n. sp.[1]

[1] Stemmadenia decipiens sp. nov., arborea glabra; foliis ovatis 7–10 cm. longis 4–7 cm. latis, petiolis 5–7 mm. longis; corollae tubo salverformo 2–3 cm. longo, lobis 1–2 cm. longis; lobis calycis ovatis inaequalibus 4–6 mm. longis 2–3 mm. latis flavis; folliculis ovato-oblongis acutibusque.—Mexico, between Rosario and Colomas, Sinaloa, July 12, 1897, *J. N. Rose 1614* (US. TYPE).

Shrubs or small trees, 2–10 m. high; leaves 7–10 cm. long, 4–7 cm. broad, glabrous, petiolate, petioles 5–7 mm. long; inflorescence 3–9-flowered; corolla yellow or yellowish white, the tube 2–3 cm. long, 4–5 mm. broad at the orifice, the limb 1–2 cm. broad; calyx about one-fifth the length of the tube, the segments 4–6 mm. long, 2–3 mm. broad, slightly imbricated in two unequal series, both series yellowish, appressed; immature follicles ovate, attenuate at the apex, mature follicles unknown.

Distribution: southern Mexico and adjacent Central America.

Specimens examined:

MEXICO:

SINALOA: between Rosario and Colomas, July 12, 1897, *Rose 1614* (US, No. 300461 TYPE, 300462); near Rosario, July 24, 1897, *Rose* (US).

OAXACA: Pochutla, April 19, 1917, *Conzatti, Reko & Makrinius 3172* (MBG).

NICARAGUA: Managua, 1925, *René 78* (MBG).

This species has been called *decipiens* because it possesses the smallest calyx of the subgenus *Ochrodaphne*, thus recalling the small calyx-lobes of *S. Palmeri* in the subgenus *Eustemmadenia*, for which it has been mistaken.

10. Stemmadenia grandiflora (Jacq.) Miers, Apoc. S. Am. 75. 1878. Pl. 47, fig. 4.

Tabernaemontana grandiflora Jacq. Enum. Pl. Carib. 14. 1762; L. Mant. 53. 1767; Willd. Sp. Pl. **1**²: 1245. 1798; Lam. Dict. **7**: 528. 1806; Roem. & Schult. Syst. **4**: 428. 1819; A. DC. in DC. Prodr. **8**: 368. 1844; G. Don, Gen. Syst. **4**: 88. 1887; Sesse & Mocino, Fl. Mex. 431. 1894; Ramirez, Pl. Mex. 155. 1902; Pulle, Enum. Vasc. Pl. Sur. 381. 1906; Standl. Contr. U. S. Nat. Herb. **27**: 308. 1928.

Shrubs or small trees; leaves 6–8 cm. long, 3–5 cm. broad, glabrous, petiolate, petioles 5–7 mm. long; inflorescence 2–9-flowered; corolla yellowish white, the tube 3–3.5 cm. long, 4–5 mm. broad at the orifice, the limb 1.5–2 cm. broad; calyx about one-third the length of the tube, the segments 8–12 mm. broad, 10–15 mm. long, closely imbricated in two unequal series, both

series green, spreading; follicles 3–3.5 cm. long, 2–3 cm. broad, acute at the apex.

Distribution: tropical forests, southern Mexico, Central America, and northeastern South America.

Specimens examined:

MEXICO:

SINALOA: Colomas, July 16, 1897, *Rose 1711* (US); near Colomas, July 14–17, *Rose* (US).

NAYARIT: vicinity of Acaponeta, Tepic, April 12, 1910, *Rose, Standley & Russell 14484* (US).

COSTA RICA: exact locality and date lacking, *Tonduz 17653* (US).

PANAMA: Chagres, Jan.–March, 1850, *Fendler 234* (G, MBG); exact locality and date lacking, *Duchassaing* (G); Puerto Remedios, Chiriqui, March 31, 1911, *Pittier 3388* (NY, US); Fato, Dept. Colon, along the beach, July 8–10, 1911, *Pittier 3940* (US); David, Chiriqui, Feb. 25, 1911, *Pittier 2824* (US); Cana, April 17, June 8, 1908, *Williams 803* (US); Cerro Gordo, near Culebra, June 29, 1911, *Pittier 3739* (US); Paso del Olá, Prov. Coclé, Dec. 7–9, 1911, *Pittier 5011* (US); Mount Hope Cemetery, Canal Zone, Dec. 28, 1923, *Standley 28840* (US); Punta Paitilla, Nov. 3, 1921, *Heriberto 209* (US); Puerto Obaldia, forests, Oct. 11, 1911, *Pittier 4406* (US); Sabana de Juan Corso, Prov. Panama, near Chepo, Sept. 1911, *Pittier 4748* (US); Panama City, old Experiment Station, June 13, 1923, *Maxon, Harvey & Valentine 7084* (US); Bella Vista, near Panama City, June 12, 1923, *Maxon & Valentine 6948* (US); Juan Diaz, Prov. Panama, near Tapia River, June 1–3, 1923, *Maxon & Harvey 6751 & 6646* (US); Corozal, Canal Zone, Aug. 1924, *Stevens 90* (US); Chivi-Chivi Trail, 2 mi. above Red Tank, Canal Zone, May 28, 1923, *Maxon & Harvey 6599* (US); Barro Colorado Is., Canal Zone, Aug. 18, 1927, *Kenoyer 500* (US); Changuinola Valley, 1927, *Cooper & Slater 63a* (US); Taboga Is., Feb. 26, 1923, *Macbride 2798 & 2799* (US); Barro Colorado Is., Canal Zone, Nov. 18–24, 1925, *Standley 40994* (US).

VENEZUELA: Tovar Colony, Aug. 16, 1855, *Fendler 1027* (G, NY); San Martin, on the Rio de Palomar, Oct. 15, 1922, *Pittier 10516* (G); between La Guaira and Rio Grande, June 12, 1917,

Curran & Haman 971 (G, US); San José & Rio Chico, June 16, 1913, *Pittier 6355* (NY); Cierucunté, April 10, 1922, *Pittier 10288* (NY); La Guavia, July 4, 1900, *Robinson & Lyon* (US); Puerto La Cruz, April, 1914, *Jahn 336* (US); Rio Chico, Miranda, June 20, 1923, *Jahn 1280* (US); between San José and Las Trincheras, Fed. Dist. (Caracas), Oct. 4, 1921, *Pittier 11* (US); Curucuti, March 19, 1918, *Pittier 7774* (US); Perijá, Zulia, 1917, *Tejera 14* (US).

COLOMBIA: Turbaco, Nov. 1920, *Heriberto 461* (US); Cartagena, 1919, *Heriberto 249* (US); between Ciénaga de Santa Marta and the foothills, June 22–30, 1906, *Pittier 1594* (US, NY); San Martin de Loba and vicinity, Bolivar, April–May, 1916, *Curran 12* (US); Santa Marta, 1898–1901, *H. H. Smith 1639* (MBG, NY, ANSP, US).

DUTCH GUIANA: Paramaribo, on way to Kwatta, *Samuels* (US); Paramaribo, forests on the way to the farm of Kwatta, April 27, 1916, *Samuels 384* (G); Paramaribo, forest behind Gongrypstreet, April 12, 1916, *Samuels 385* (G); Paramaribo, May 10, 1905, *Mayo* (ANSP); "Surinam," *Weigelt* (ANSP).

This common species is known popularly in Panama as "Huevo de Gato," "Lechosa," and "Venenillo"; in Venezuela as "Hueves de Burro"; and in Mexico as "Lechoso." Called "yellow laurel" by G. Don.

11. **Stemmadenia pauciflora** Woodson, n. sp.[1] Pl. 49, fig. 1.

Shrubs or small trees; leaves 8–12 cm. long, 2.5–5 cm. broad, glabrous, petiolate, petioles 2–3 mm. long; inflorescence 1-flowered by abortion; corolla yellow or yellowish white, salverform, the tube 3–4 cm. long, 3–4 mm. broad at the orifice, the limb 1–1.5 cm. broad; calyx about one-fourth the length of the tube, the segments 7–9 mm. long, 6–9 mm. broad, strongly imbricated in two unequal series, both series green; follicles unknown.

Distribution: north-central Colombia and Guiana.

[1] **Stemmadenia pauciflora** sp. nov., arborea glabra; foliis oblongo-lanceolatis 8–12 cm. longis 2.5–5 cm. latis, petiolis 2–3 mm. longis; cymis unifloris abortivis; corollae tubo salverformo 3–4 cm. longo, lobis 1–1.5 cm. longis; lobis calycis ovatis inaequalibus 7–9 mm. longis 6–9 mm. latis viridis; folliculis ignotis.—Colombia, between Espinal and Cuamo, Tolima, open loam along stream, alt. 350–400 m., July 21, 1917, *Pennell & Rusby 186* (NY TYPE).

Specimens examined:

COLOMBIA: open loam along stream, between Espinal and Cuamo, alt. 350–400 m., Tolima, July 21, 1917, *Pennell & Rusby 186* (NY TYPE).

DUTCH GUIANA: "in sylvis pr. urbem Paramaribo," March–April, 1844, *Kappler 1565* (MBG).

Stemmadenia pauciflora, so-called because of the singularly reduced inflorescence, is equally distinct because of the short corolla-limb. At present the two specimens referable to the species constitute a rather scattering range, but doubtless with increased collecting activity additional localities will become known. The young inflorescence is normally composed of several buds, all of which abort very early except the one destined to produce the fully-developed flower. This character of the inflorescence is demonstrated nicely by the two above-cited specimens. Upon *Kappler 1565* three inflorescences appear, one with one aborting and one developing bud, and two with full-blown flowers and one aborted bud each. *Pennell & Rusby 186* likewise demonstrate this remarkable propensity. On that sheet (NY) three inflorescences appear, one with one aborting and one developing bud, another with two aborted and one developing bud, and another with a full-blown flower and one aborted bud.

12. Stemmadenia Pennellii Woodson, n. sp.[1]

Shrubby vines (?) or shrubs; leaves 7–9 cm. long, 3–4 cm. broad, glabrous or glabrate above, beneath softly rufous-puberulent, petiolate, petioles 1–3 mm. long; inflorescence 2–4-flowered; corolla salverform, yellow, the tube 3–3.5 cm. long, the limb 2.5–3 cm. broad; calyx-lobes in two very unequal series, the inner about 2 cm. long, the outer 1.2–1.5 cm. long, 7–10 mm. broad, strongly imbricated; follicles unknown.

[1] Stemmadenia Pennellii sp. nov., arborea vel vinea frutescens (?), foliis oblongo-lanceolatis 7–9 cm. longis 3–4 cm. latis supra glabris vel glabratis subtus rufo-puberulentis; petiolis 1–3 mm. longis; corollae tubo salverformo 3–3.5 cm. longo, lobis ca. 2.5 cm. longis; lobis calycis majusculis inaequalibus 2-serialibus, inferioris ca. 2 cm. longis superioris 1.2–1.5 cm. longis, virido-flavibus; folliculis ignotis.—Colombia, Turbaco, Bolivar. Shrubby vine, thin loam over white rock, alt. 150–200 m., March 27, 1918, *Pennell 4755* (Gray Herb. TYPE).

Distribution: southern Mexico and northern Colombia.

Specimens examined:

Mexico:

Guerrero: Achatla, May, 1926, *Reko 4892* (US).

Colombia: Turbaco, Bolivar. Shrubby vine. Thin loam over white rock, alt. 150–200 m., March 27, 1918, *Pennell 4755* (G type, US, F, MBG).

This species, although closely related to *S. grandiflora*, is very distinctive, not only because of the strikingly unequal calyx-lobes, but because of the rufous puberulence of the leaves. The flowers, also, appear to be more turbinate in the reflexion of the corolla-lobes than any other species of *Ochrodaphne*, but this character has not been noted because most of the specimens of that subgenus are so poorly pressed, and Dr. Pennell's are so carefully prepared, that use of this character would be dangerous. The species is dedicated to Dr. Francis W. Pennell, of the Academy of Natural Sciences of Philadelphia, the collector of the type specimen.

13. Stemmadenia eubracteata Woodson, n. sp.[1] Pl. 49, fig. 2.

Shrubs or small trees; leaves 6–8 cm. long, 2–3 cm. broad, glabrous, petiolate, the petioles 4–5 mm. long; inflorescence 2–5-flowered; corolla salverform, yellow, the tube about 2.5 cm. long, the limb about 1.5 cm. broad; calyx-lobes 3–4 mm. broad, 8–10 mm. long, all green, spreading; bracts semifoliaceous; follicles unknown.

Distribution: known only from the type locality in Guatemala.

Specimens examined:

Guatemala: Volcan Tecuamburro, Dept. Santa Rosa, alt. 2000 m., Feb. 1893, *Heyde & Lux 4538* (G type).

This species is one of the most remarkable species of *Ochrodaphne* by reason of the spreading calyx, the narrow leaves, and above all the curiously foliaceous bracts, which are absolutely different from those of any other species of the genus *Stemmadenia*.

[1] **Stemmadenia eubracteata** sp. nov., arborea; foliis lanceolatis 6–8 cm. longis 2–3 cm. latis glabris, petiolis 4–5 mm. longis; corollae tubo salverformo 2.5 cm. longo, lobis ca. 1.5 cm. longis; lobis calycis 3–4 mm. latis 8–10 mm. longis; bracteis semifoliaceis; folliculis ignotis.—Guatemala, Volcan Tecuamburro, Dept. Santa Rosa, alt. 2000 m., Feb., 1893, *Heyde & Lux 4538* (Gray Herb. type).

14. Stemmadenia Robinsonii Woodson, n. sp.[1]

Shrubs or small trees; leaves 12–16 cm. long, 4–5 cm. broad, glabrous, petiolate, the petioles 1–3 mm. long; inflorescence 2–3-flowered; corolla salverform, yellow, the tube 2–2.5 cm. long, the limb about 1–1.5 cm. broad; calyx-lobes linear-lanceolate, 1.5–2 cm. long, 3–4 mm. broad, very slightly imbricated in two unequal series, both series yellow, appressed; follicles unknown.

Distribution: known only from the type locality in Costa Rica.

Specimens examined:

COSTA RICA: Talamanca Mts., March, 1894, *Pittier 8617* (US TYPE).

This species is dedicated to Dr. B. L. Robinson, who, in 1899, questioned its determination as *S. bella* Miers, and called attention in a note upon the specimen to the peculiar calyx, which is the most striking characteristic of the species. In addition to the calyx, *S. Robinsonii* differs from its nearest relative, *S. Donnell-Smithii*, in the leaves, which are glabrous and oblong-lanceolate in the former, and spatulate and barbate in the latter.

15. Stemmadenia Donnell-Smithii (Rose) Woodson, n. comb.

Tabernaemontana Donnell-Smithii Rose, Bot. Gaz. **18**: 206. 1893.

Tabernaemontana Donnell-Smithii Rose var. *costaricensis* Donn.-Sm. Bot. Gaz. **24**: 397. 1897.

Shrubs or small trees; leaves 6–8 cm. long, 3–3.5 cm. broad, spatulate, minutely glandular-puberulent or glabrate above, beneath conspicuously barbate in the axils of the midvein, petiolate, the petioles 1–2 mm. long; inflorescence 1–4-flowered; corolla yellow, salverform, the tube 2.5–3 cm. long, the limb 1.5–2 cm. long; calyx nearly equalling the length of the corolla-tube, 2–2.5 cm. long, the lobes 1.5–2 cm. broad, in two closely imbricated yellowish series; follicles about 3.5 cm. long, about 3 cm. broad, rounded at the apex.

[1] Stemmadenia Robinsonii sp. nov., arborea glabra; foliis oblongo-lanceolatis 12–16 cm. longis 4–5 cm. latis, petiolis 1–3 mm. longis; corollae tubo salverformo 2–2.5 cm. longo, lobis 1–1.5 cm. longis; lobis calycis linearo-lanceolatis 1.5–2 cm. longis 3–4 mm. latis; folliculis ignotis.—Costa Rica, Talamanca Mts., March, 1894, *Pittier 8617* (US TYPE).

Distribution: tropical forests, southern Mexico and Central America.

Specimens examined:

Mexico: locality and date lacking, *Gregg 893* (MBG).

Guerrero: La Correa, Oct. 5, 1898, *Langlassé 427* (G, US).

Costa Rica: Nicoya, April, 1900, *Tonduz 13904* (G, NY); Santa Clara, Sept. 1896, *Cooper 10241* (US); Matambú, Nicoya Peninsula, May 23, 1903, *Cook & Doyle 706* (US); Nicoya, alt. 200 m., May 22, 1903, *Cook & Doyle 686* (US); Nicoya, forests, *Tonduz 13904* (US); Capulín, on the Rio Grande de Taracales, Prov. Alojuela, April 2, 1924, *Standley 40220* (US); Arenal, May 5, 1922, *Valerio 86* (US).

British Honduras: Middlesex, Jan. 17, 1926, *Ricard 13* (US).

Honduras: Ceiba, Aug. 20, 1916, *Dyer A84* (US).

Nicaragua: Las Nubes, June 28, 1923, *Maxon, Harvey & Valentine 7502* (US).

Guatemala: St. Thomas, May 29, 1909, *Deam 6052* (G); Escuintla, alt. 1100 ft., March, 1890, *Donnell-Smith 2404* (G); San Felipe, Dept. Retalhulen, alt. 2050 ft., April, 1892, *Donnell-Smith 2763* (G, US type, NY, F, MBG); Barranca de Eminencia, Dept. Amatitlan, alt. 1400 ft., Feb. 1892, *Donnell-Smith 2762* (G, NY, MBG); Escoba, June 2, 1922, *Standley 2462* (US); Hacienda el Baul, Dept. Escuintla, March 2, 1921, *Tonduz & Rojas 36* (US); Santa Lucia, Escuintla, March 2, 1905, *Kellerman 5286 & 5275* (US); Mazatenango, border of forest, Feb. 19, 1905, *Maxon & Hay 3490* (US); San Jose de Escuintla, April, 1892, *Donnell-Smith 2765* (US); San Juan Mixtan, April, 1890, *Donnell-Smith 2405* (US); Primavera, Dept. Sololá, Oct. 1891, *Shannon 120* (US); Rio Toro Amarillo, Llanuras de Santa Clara, April, 1896, *Donnell-Smith 6646* (US type var. *costaricensis*); Santa Barbara, Dept. Sololá, Aug. 1891, *Shannon 152* (US); Naranjo, Dept. Escuintla, March, 1892, *Donnell-Smith 2764* (US).

El Salvador: vicinity of San Salvador, alt. 650–850 m., Dec. 20, 1921–Jan. 4, 1922, *Standley 19187* (US, G, NY); vicinity of Izalco, Dept. Sonsonate, March 19–24, 1922, *Standley 21865* (G, US); same locality and date, *Standley 22218* (G, NY, US); vicinity of Ixtepeque, Dept. San Vicente, alt. 400 m.,

March 6, 1922, *Standley 21463* (G, US); San Salvador, 1921, *Calderon 187* (NY, US); San Salvador, 1900, *Renson 106* (US); Armenia, Dept. Sonsonate, April 18, 1922, *Standley 23452* (US); Dept. Ahuachapán, 1923, *Padilla 331* (US); Izalco, Dept. Sonsonate, Feb. 17, 1907, *Pittier 1936* (US).

In referring this species to the genus *Tabernaemontana*, Dr. Rose[1] was fully cognizant of its affinities, and especially of its relation to *Stemmadenia grandiflora*, but preferred to assign it to the former genus, remarking "*T. grandiflora*, as is known, was referred by Miers to *Stemmadenia*, but is retained by Mr. Hemsley in *Tabernaemontana*. The difference between these two genera is sometimes a little difficult to determine." Dr. Rose further added an interesting note concerning the species: "Capt. Smith observes of this plant: 'It is not exactly a tree in habit. It occurred everywhere as I went from the coast up to the slopes of the volcanoes at an elevation of 5,000 ft. The natives call it *Cobal* (varnish gum).' Other popular names for the species are 'Cojón' and 'Cojón de puerco.'"

The observations of Dr. Rose quoted above are representative of the attitude with which the majority of botanists have regarded the genus *Stemmadenia*. This paper will be successful if merely it demonstrates the numerous precise differences between the genera *Tabernaemontana* and *Stemmadenia*.

Excluded Species

Stemmadenia guatemalensis Müll.-Arg. Linnaea **30**: 410. 1859. = **Malouetia guatemalensis** (Müll.-Arg.) Standl. Jour. Wash. Acad. Sci. **15**: 459. 1925. (*Malouetia panamensis* Müll.-Arg. in Van Heurck, Pl. Nov. 185. 1871.)

List of Exsiccatae Cited

The distribution numbers are printed in *italics;* collections distributed without numbers are indicated by a dash. The numbers in parentheses indicate the species numbers in the present revision.

Baker, C. F. *2270* (4).
Bilimek, —, *269* (7).
Botteri, M. *988* (7).
Bourgeau, M. *2440* (7).
Brenes, A. M. *14275*, *14278* (6).
Calderón, S. *1230* (4); *187* (15).
Chaves, D. *215* (4).
Conzatti, C. & Reko, B. P. *3258* (4a).
Conzatti, C., Reko, B. P. & Makrinius, M. *3172* (9).
Cook, O. F. & Doyle, C. B. *723* (4a); *120*, *152*, *706*, *686* (15).

[1] Rose, Bot. Gaz. **18**: 206. 1893.

Cooper, G. P. *10241* (15).
Cooper, G. P. & Slater, G. M. *63a* (10).
Curran, H. M. *12* (10).
Curran, H. M. & Haman, S. *971* (10).
Deam, C. *6070* (4a); *6052* (15).
Donnell-Smith, J. *1800* (7); *2404*, *2405*, *2762*, *2763*, *2764*, *2765*, *6646* (15).
Duchassaing, E. P. —, (10).
Dyer, F. J. *A84* (15).
Fendler, A. *1027* (10).
Galeotti, H. *1599*, *1605* (7).
Gaumer, G. F. *23204* (7).
Goldman, E. A. *358* (1a); *1027* (4a); *575* (7).
Gregg, J. *893* (15).
Greenman, J. M. & Greenman, M. T. *5713*, *5920* (4a).
Hartmann, C. V. *534*, *1032* (1a).
Hayes, S. — (3).
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Jones, M. E. *335* (1a).
Kappler, A. *1565* (11).
Kellerman, W. A. *4511* (4a); *5286*, *5275* (15).
Kenoyer, L. A. *500* (10).
Lamb, F. H. *467* (2).
Langlassé, E. *1029* (4); *427* (15).
Macbride, J. F. *2798*, *2799* (10).
Maxon, W. R. *7647*, *7727* (3).
Maxon, W. R. & Harvey, A. D. *6599*, *6646*, *6751* (10).
Maxon, W. R., Harvey, A. D. & Valentine, A. T. *7270*, *7539* (3); *7542* (4); *6948*, *7084*, *7502* (10).
Maxon, W. R. & Hay, R. *3766* (4a); *3490* (15).
Maxon, W. R. & Valentine, A. T. *6948* (10).
Mell, C. D. *28* (4a).
Mexia, Y. *733*, *1490* (1a).
Mille, L. *59* (4a).
Millspaugh, C. F. *27* (7).
Montes, M. N. & Salazar, A. E. *405*, *268* (1a).
Ortega, J. G. *4175* (1a).
Padilla, S. A. *331* (15).
Palmer, E. *M.* (1a); *132*, *1470* (1a).
Pennell, F. W. *4755* (12).
Pennell, F. W. & Rusby, H. H. *186* (11).
Pittier, H. *1177* (4); *133*, *2908* (4a); *11094* (5); *11*, *1594*, *2824*, *3388*, *3739*, *3940*, *4406*, *4748*, *5011*, *6355*, *7774*, *10288*, *10516* (10); *8617* (14); *1936* (15).
Popenoe, W. *977* (4a).
Pringle, C. G. *4370* (1); *5151*, *5363*, *6847*, *6872* (1a); *8103* (7).
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Ricard, B. H. *13* (15).
Robinson, A. & Lyon, M. W., Jr. — (10).
Rose, J. N. *1573*, *1688*, *2888*, *3260* (1a); —, *1614* (9); —, *1711* (10).
Rose, J. N. & Hough, W. *4777* (1a).
Rose, J. N., Painter, J. H. & Rose, J. S. *9274* (4a).
Rose, J. N. & Rose, G. *23612* (4a).
Rose, J. N., Standley, P. C. & Russell, P. G. *13874* (1); *14064*, *14544*, *14675* (1a); *14484* (10).
Rusby, H. H. *931*, *1163* (4a).
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Schott, A. *430* (7).
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Shannon, W. C. *5042* (4a); *120*, *152* (15).
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Smith, H. H. *1639* (10).
Standley, P. C. *20686*, *20713*, *20943*, *32793*, *35459* (3); *21034* (4); *22372*, *22539* (4a); *28840*, *40994* (10); *19187*, *21463*, *21865*, *22218*, *23452*, *2462*, *40220*, *40994* (15).
Stevens, F. L. *90* (10).
Tejera, E. *14* (10).
Tonduz, A. *13900* (4a); *17653* (5); *13904* (15).
Tonduz, A. & Rojas, A. *147* (7); *17653* (10); *36* (15).
Tuerckheim, H. von. *981* (7).
Valerio, J. *86* (15).
Weigelt, C. — (10).
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Explanation of Plate

PLATE 47

Fig. 1. Habit of *Stemmadenia glabra*. × ½.
Fig. 2. Habit of *Stemmadenia Galeottiana*. × ½.
Fig. 3. Detail of floral mechanism of *Stemmadenia Galeottiana*. × 2.
Fig. 4. Habit of *Stemmadenia grandiflora*. × ½.
Fig. 5. Fruit of *Stemmadenia tomentosa* var. *Palmeri*. × ½.

WOODSON—STUDIES IN APOCYNACEAE

Explanation of Plate

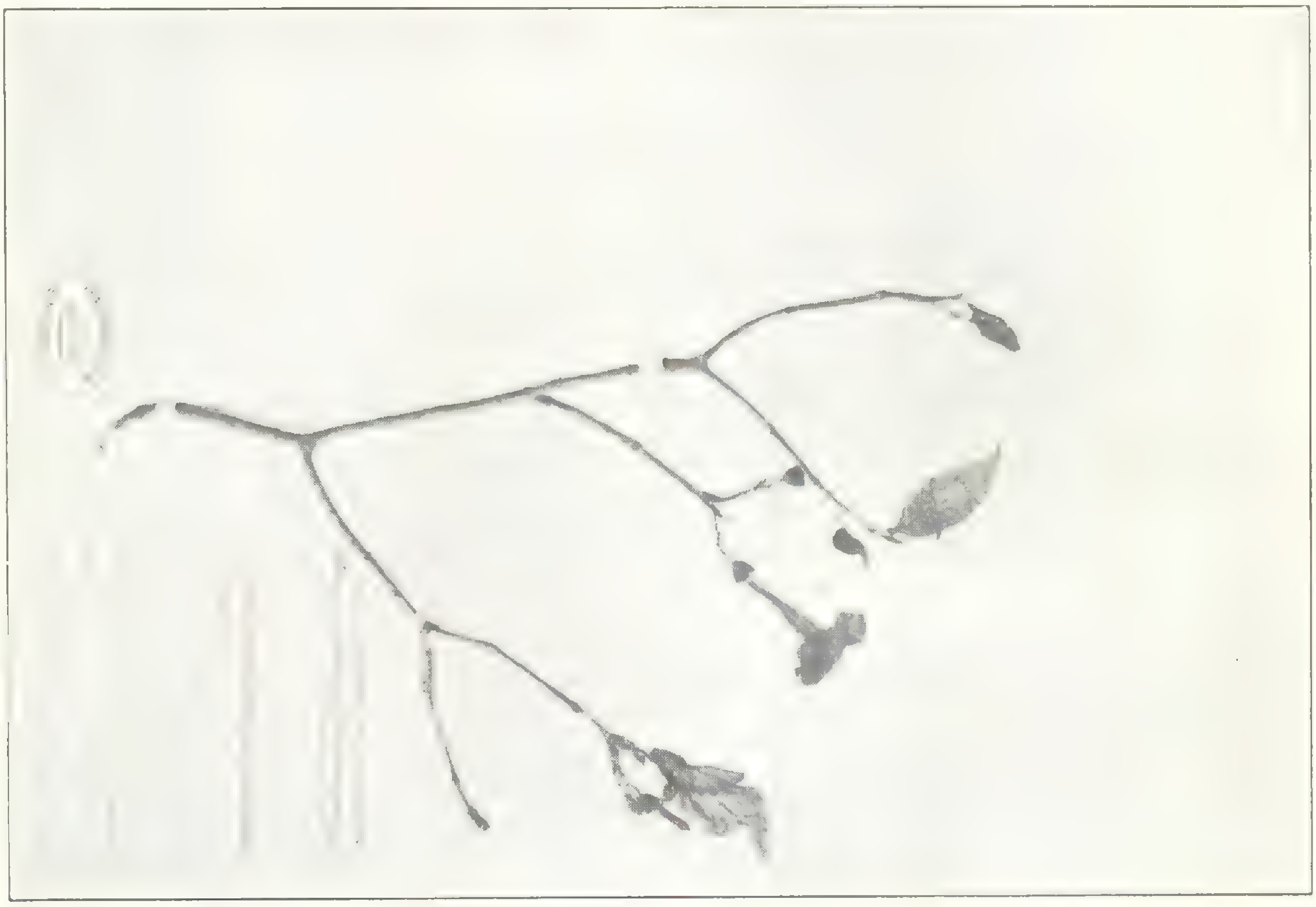
PLATE 48

Fig. 1. *Stemmadenia sinaloana* Woodson, from the type specimen, *F. H. Lamb No. 467*, in the Gray Herbarium of Harvard University.

Fig. 2. *Stemmadenia Greenmanii* Woodson, from the type specimen, *Brenes 14275*, in the Gray Herbarium of Harvard University.

1

2



WOODSON—STUDIES IN APOCYNACEAE

Explanation of Plate

PLATE 49

Fig. 1. *Stemmadenia pauciflora* Woodson, from the type specimen, *Pennell & Rusby No. 186*, in the Herbarium of the New York Botanical Garden.

Fig. 2. *Stemmadenia eubracteata* Woodson, from the type specimen, *Heyde & Lux No. 4538*, in the Gray Herbarium of Harvard University.

1

2

WOODSON—STUDIES IN APOCYNACEAE

STUDIES IN THE APOCYNACEAE. III

A Monograph of the Genus Amsonia

ROBERT E. WOODSON, JR.

Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

Historical Discussion

When the second edition of Linnaeus's 'Species Plantarum' appeared in 1762, one of the many additions to the species presented in the first edition (1753) was *Tabernaemontana Amsonia,*[1] a plant the exact genus of which Linnaeus himself was not precisely sure, qualifying it to the genus *Tabernaemontana* with the remark "Affinis Camerariae et Tabernaemontanae." The attitude with which Linnaeus treated his *Tabernaemontana Amsonia* is essayed by Sir J. E. Smith,[2] and throws much illumination upon problems concerning the genus which will receive subsequent treatment in this monograph: "Tabernaemontana ——. The herbaceous plants, supposed by Linnaeus to belong to this genus, constitute, as we have already said, and as Linnaeus himself originally thought, a very distinct one, of which we shall now treat by the name of Amsonia. We can give no positive account of the meaning or origin of this word except that its author, according to Miller,[3] was Clayton. Linnaeus in his own copy of Gronovius' Flora Virginica, ed. 1. p. 26, has written *Amsonia* as a generic name, to what Clayton took for a species of *Nerium,* and has subjoined also in manuscript the characters of the follicles and seeds. This plant, in the second edition of the Species Plantarum, is the *T. Amsonia;* and so it remained until Mr. Walter restored it to rank as a genus; but without throwing any light upon the name."

The name *Amsonia* has indeed been an enigma, and Rafin-

[1] L. Sp. Pl. ed. 2, **2**: 301. 1762.

[2] Sm. in Rees, Cycl. **35**. 1819.

[3] Miller, Gard. Dict. ed. 5, **2**[2]: art. "Tabernaemontana." 1807.

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esque[1] even went so far as to change the name to "*Ansonia*," referring to the passage above quoted from Smith, and naively remarking that he had been acquainted with several Ansons, but never an Amson, and so the name must be misspelled.

With the fresh stimulus of Rafinesque's contention a special search was made for the origin of the name *Amsonia*, and for a time it appeared that Rafinesque's intuition had been well guided, for, although all of the published floras and manuals dealing with the genus spoke readily of "Dr. Amson, a colonial physician," or "Charles Amson, a physician of South Carolina," no authentic trace of that gentleman could be found, either in published encyclopedias or standard reference works. Historical societies in Virginia and the Carolinas were invoked to no avail. An Amson, any Amson whatever, was not forthcoming.

However, Ansons were frequent, including a certain Lord George Anson, a royal governor fond of explorative expeditions, from one of which he had discovered and brought to civilization a new esculent pea. Rafinesque was about to be vindicated, when a letter from Clayton to John Bartram appeared which seems to solve the problem, although not completely. The letter, which was written from Gloucester County, Virginia, Sept. 1, 1760, follows:

"Dear Friend:

"I have sent you, enclosed, some seed of a new plant, which I presume is a stranger in your northern part of the world. Indeed it grows here only in the southern parts of the colony. I have it in my garden, but have quite forgotten whether I showed it to you, when I had the favor of your company. If I did, I believe I told you it was to be called *Amsonia*, after a doctor, here; but I think the name inscribed upon the inclosed more proper, as it answers to the particular form of its seed.

"I intend to send you some of the seed of our thorny Sensitive Plant by the first opportunity that offers, after it is ripe;

"And remain, dear sir, your sincere friend
"And most most humble servant,
"JOHN CLAYTON."

[1] Raf. New Fl. N. Am. 4: 58. 1838.

Allowing for orthographical errors, then, *Amsonia* was definitely named for a certain Dr. Amson, a physician of Gloucester Co., Virginia; but regarding his complete name, or the positive form of spelling of his family name, doubt still remains. Lord Anson, however, can undoubtedly be discarded as a possibility. The "name inscribed upon the inclosed," which Clayton thought to be "more proper," was evidently *Tabernaemontana Amsonia.*

Tabernaemontana Amsonia was immediately conspicuous among the other Tabernaemontanas both in habit and in habitat, since it was the only temperate herbaceous member of the genus, and in 1788 attracted the attention of Thomas Walter,[1] who described from it a new genus, naming the type species, in transposition of the Linnaean combination, *Amsonia Tabernaemontana.* At the same time, Walter[2] also described a new plant from the Carolinas which he assigned to the same new genus, calling it *A. ciliata.*

As a result of his explorations in the southeastern United States, André Michaux[3] was able to expand the little genus with the addition, in 1803, of two new species, *A. latifolia* and *A. angustifolia.* The latter was a transfer to *Amsonia* of a species placed in the genus *Tabernaemontana* by Aiton[4] in 1789. Pursh,[5] in 1814, also published a new species which he named *A. salicifolia.*

Probably the most interesting addition which has ever been made to the species of *Amsonia* was in 1819, when Roemer and Schultes[6] transferred to that genus a plant which had been assigned to *Tabernaemontana* by Thunberg[7] in 1784. The species, *A. elliptica,* was a native of Japan, and is yet the only known member of the genus not native to North America. Thunberg was slightly hesitant, as was Linnaeus, in committing his plant to the genus *Tabernaemontana,* but relied upon the precedence of the earlier author, remarking, much as did Lin-

[1] Walt. Fl. Carol. 98. 1788.
[2] Walt. *l. c.* 1788.
[3] Michx. Fl. Bor. Am. **1**: 121. 1803.
[4] Ait. Hort. Kew. **1**: 300. 1789.
[5] Pursh, Fl. Am. Sept. ed. 1, **1**: 184. 1814.
[6] Roem. & Schult. Syst. Veg. **4**: 432. 1819.
[7] Thunb. Fl. Jap. 111. 1784.

naeus, "Valde affinis Amsoniae," a significant statement in the light of the later disposition of the species.

The same year there appeared in the Rees 'Cyclopaedia' the description by Sir J. E. Smith[1] of a species of *Amsonia* which he called *A. tristis*. The plant was reported grown in an English garden from seed collected in North America by Lyon, who contributed the plant from which Pursh published his *A. salicifolia*. Smith gave to his plant the common name "brownish-flowered Amsonia," since, as he wrote, "The flowers . . . are of a dingy brown hue, the segments of their limb strongly reflexed, at least in fading." The species has not been reported since its publication, and because of the rather suspicious-sounding description of the flowers, the name has generally been referred to as a synonym of *A. Tabernaemontana* Walt., or of *A. salicifolia* Pursh.

Rafinesque's 'New Flora of North America' appeared in 1838, with a comparative sketch of the "Ansonias" then recognizable, and added one new species, *A. tenuifolia*,[2] the originality of which the author took unusual pains to indicate.

In the 'Prodromus' of De Candolle the genus *Amsonia* received its first collective treatment. Besides recognizing the species which had previously been published with the exception of *A. tenuifolia* Raf., Alphonse De Candolle[3] described a new plant which he termed *A. salicifolia* Pursh var. *ciliolata*, from Alabama and Louisiana. The following year the genus gave evidence of the growing botanical knowledge of the southwestern United States by the publication by Torrey and Frémont[4] of *A. tomentosa* from "west of the Rocky Mountains." Fourteen years later, as a result of the activities of the Mexican Boundary Survey, Torrey[5] published a second species, *A. longiflora*, a very distinct plant of the region about El Paso, Texas.

Some time later the genus came to the attention of Asa Gray during the course of the preparation of the 'Synoptical Flora,'

[1] Sm. in Rees, Cycl. **35**: end of art. "Tabernaemontana." 1819.
[2] Raf. New Fl. N. Am. **4**: 58. 1838.
[3] A. DC. in DC. Prodr. **8**: 384. 1844.
[4] Torr. & Frém. in Frém. Rept. 1843–1844, 316. 1845.
[5] Torr. in Rept. Mex. Bound. Surv. **2**[1]: 159. 1859.

and in 1877[1] he published two new species from the Southwest, *A. brevifolia* and *A. Palmeri*. The following year when the 'Synoptical Flora'[2] was issued, there appeared also a new variety of the genus which Gray termed *A. angustifolia* Michx. var. *Texana*. Besides being noteworthy for the contribution of a new variety, Gray's treatment of *Amsonia* in the 'Synoptical Flora' constitutes a scientific and comprehensive treatment of the group in its phylogenetic aspects.

In 1894, in accordance with the Rochester Code of Nomenclature, a double name was made by Britton[3] for the type species of the genus. This name, *Amsonia Amsonia*, is still current among some botanists.

K. Schumann,[4] in Engler and Prantl's 'Natürlichen Pflanzenfamilien,' elaborated upon Gray's treatment in the 'Synoptical Flora' and divided the genus into two sections which he called *Euamsonia* and *Sphinctosiphon*. In the first section, three species were recognized, namely, *A. Tabernaemontana* Walt., *A. ciliata* Walt., and *A. elliptica* (Thunb.) Roem. & Schult., and in the second section, four species, *A. Palmeri* Gray, *A. longiflora* Torr., *A. brevifolia* Gray, and *A. tomentosa* Torr. & Frém.

In the twentieth century numerous additions have been made to the genus *Amsonia*. In 1900 A. A. Heller[5] elevated Gray's *A. angustifolia* Michx. var. *Texana* to specifie rank. In Small's 'Flora of the Southeastern United States' two new species are contained, *A. ludoviciana* Vail[6] and *A. rigida* Shuttleworth.[7] Other new specific contributions have been *A. latifolia* M. E. Jones,[8] 1908, *A. Eastwoodiana* Rydberg,[9] *A. arenaria* Standley,[10] and *A. hirtella* Standley,[11] in 1913. Jepson,[12] in 1925, reduced *A. tomentosa* Torr. to a variety of *A. brevifolia* Gray.

[1] Gray, Proc. Am. Acad. **12**: 64. 1877.
[2] Gray, Syn. Fl. N. Am. **2**[1]: 81. 1878.
[3] Britton, Mem. Torr. Bot. Club **5**: 262. 1894.
[4] K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**[2]: 143. 1895.
[5] Heller, Muhlenbergia **1**: 2. 1900.
[6] Vail, in Small, Fl. Southeast. U. S. 935. 1903.
[7] Shuttlew. in Small, *l. c.* 1903.
[8] Jones, Contr. West. Bot. **12**: 50. 1908.
[9] Rydb. Bull. Torr. Bot. Club **40**: 465. 1913.
[10] Standl. Proc. Biol. Soc. Wash. **26**: 117. 1913.
[11] Standl. *l. c.* 1913.
[12] Jepson, Man. Fl. Pl. Cal. 768. 1925.

Evidently the first printed illustration of an *Amsonia* was one presumably of *A. Tabernaemontana* in Plukenet, *t. 115, fig. 3*, 1769, where it appears as "Apocynum Virginianum Asclepiadisfolio erectum floribus pallide caeruleis radici crassa."

Because of the peculiar distribution of the genus as well as because of its growing need for a taxonomical revision, it was thought appropriate that a rather broad study be made of the genus *Amsonia*. Such a study was begun at the Gray Herbarium of Harvard University under the oversight of Dr. B. L. Robinson and Prof. M. L. Fernald, and completed at the herbarium of the Missouri Botanical Garden under Dr. J. M. Greenman. To Professors Robinson, Greenman, and Fernald, the author wishes to express his obligations most heartily for their kindly criticism and their ready suggestions. To Mr. T. H. Kearney the author is also indebted for much valuable aid with regard to the difficult species of the southwestern United States. Various herbaria have been visited, also, or specimens have been borrowed, and to the curators of each the author would express his gratitude.

Gross Morphology

The genus *Amsonia* is one of the few members of the Apocynaceae which are temperate or subtemperate, and contains within its several species only erect perennial semi-woody herbs.

Roots.—The root system of the group is characteristically fibrous. The crowns usually become woody with increasing age, and produce numerous clustered stems. Latex tubes occur in abundance, as in all the members of the family.

Stems.—The stem system is typically that of an erect perennial and varies relatively little. A mature stem is usually divided into several branches. The species inhabiting the arid regions of the southwestern United States and northern Mexico frequently have stems which are branched to a much greater extent, and much lower upon the stem than the more temperate species of the states of the Southeast and Middle West.

Leaves.—The leaves of the genus are alternate to subverticillate, and vary greatly in size and outline. Through the succession of species, extremes are found in the leaves of *A. Tabernaemontana*, which are broadly ovate-elliptic, usually measur-

ing 3–5 cm. long and 1.5–2.5 cm. broad, petiolate and opposite, to the subverticillate leaves of *A. salpignantha*, which are linear-lanceolate to linear-filiform, measuring 2–5 cm. long and .5–4 mm. broad, and decidedly sessile. The leaves may also be glabrous to glaucous, as they are in *A. salicifolia*, or densely tomentose, as they occur in *A. tomentosa*. The leaves are always entire, and are never cordate. In only one species, *A. Tabernaemontana*, are the bases of the leaf-blades other than acute when a petiole exists.

Inflorescence.—The inflorescence is a thyrsoid or corymbose cyme. The amount and shape of the inflorescence, however, is varied. The largest inflorescence of the genus is found in *A. Tabernaemontana* var. *Gattingeri*, which frequently contains over fifty blossoms, and the smallest in *A. Palmeri*, which usually has only five or six. The inflorescence may have very inconspicuous bracteoles, as in the subgenus *Euamsonia*, or quite conspicuous bracteoles, giving the whole inflorescence a chaffy appearance, as in the subgenera *Sphinctosiphon* and *Articularia*. The inflorescence may also be surrounded by the foliage, as in *A. arenaria*, or held high above the foliage by a long, nearly leafless stalk, as in *A. ciliata* var. *tenuifolia*. Pedicels may be relatively long, as in *A. Tabernaemontana* var. *salicifolia*, or frequently lacking altogether, as in *A. longiflora*.

Calyx.—The variation in the calyx is marked. In *A. Tabernaemontana* var. *salicifolia* the calyx is 1 mm. long or less in entirety, the lobes being minutely triangular-ovate. In *A. tomentosa* the calyx is as shallow as in the former species, but the lobes are fully 3–5 mm. long and are subulate-aristate. The calyx may be glabrous or pubescent, occasionally becoming sparsely hirsute.

Corolla.—The corolla is regularly five-lobed. The tube dilates upward, and may be unconstricted, as in the subgenus *Euamsonia*, or markedly constricted at the mouth, as in the subgenera *Sphinctosiphon* and *Articularia*. Variation in the length of the tube is great, ranging from 6–8 mm. in *A. ciliata* var. *tenuifolia* and allied species, to 3–3.5 cm. in *A. longiflora* and *A. salpignantha*, which have the most conspicuous flowers of the genus. The color varies from a clear cerulean blue, tinged to tawny-white in the tube,

in most of the eastern species, to white or a faint livid greenish blue in some of the western species. The tube is always villous within, and may be pubescent or glabrous without. The lobes of the corolla are spreading, and may be ovate to narrowly lanceolate in outline. The length of the lobes varies from one-half the length of the tube to an equal length, save in the large-flowered species of the section *longiflorae* of the subgenus *Sphinctosiphon*, where the ratio of the length of the tube to that of the lobes may be from about 3 : 1 in *A. longiflora* to 5 : 1 in *A. salpignantha*.

Stamens.—The stamens number five, and are adnate to the corolla-tube well above the middle. The anthers are ovate-lanceolate, acute above, obtuse below, unappendaged, and fertile throughout their entire length. The stamens are free from the stigmatic-cap.

Pistil.—The two carpels of the gynoecium, which are uniloculate and contain many two-seriate anatropous ovules, are united by a common filiform style, which is about the length of the corolla-tube, to a position immediately below the stamens, where it is surmounted by a stigmatic-cap bearing the stigma. The stigmatic-cap is constructed in three elements, the lower of which is a reflexed membranaceous appendage, originating from the summit of the stylar shaft, the central, a tangled mass of short papillae, and the upper, the stigma itself, which may be depressed-capitate or truncate, as in the subgenus *Euamsonia*, or apiculate by two distinct obtuse lobes, as in the subgenera *Sphinctosiphon* and *Articularia*.

Fruit.—The fruit of *Amsonia* is a pair of follicles which are cylindrical and acuminate, and may be slender and continuous, as in the subgenera *Euamsonia* and *Sphinctosiphon* or torose and definitely articulated into thickish constricted segments, as in the subgenus *Articularia*. In either case the seeds are one-seriate, cylindrical, and unappendaged, but in *Articularia* the endosperm is conspicuously thicker and more corky than in the endosperm of the other subgenera.

Systematic Position

The genus *Amsonia* is placed in the tribe Plumeroideae of the Apocynaceae because of its free unappendaged stamens.

The characters of an ovary containing six to many ovules, an eglandular calyx, coriaceous fruit, a hypercraterform corolla, and included stamens moreover place the genus in the subtribe Euplumeroideae.

The closest related genus to *Amsonia* appears to be for various reasons *Haplophyton.* The two genera are found in common territory from southern California to southwestern Texas. Morphologically the greatest dissimilarity lies in the seeds which are appendaged in *Haplophyton.* The leaves, which serve to aid the differentiation of the two genera in the 'Synoptical Flora,'[1] are not as widely separated as is ordinarily to be supposed, since they are not absolutely opposite in *Haplophyton* and alternate in *Amsonia,* but are more nearly approximate in the former and frequently subverticillate in the latter. The stamens are nearly alike in both genera, but are somewhat larger in *Haplophyton.* The character of the stigmatic head in that genus is also much like that of the stigmatic-head in the subgenus *Euamsonia* of *Amsonia,* although more elongate, but lacks a membranaceous reflexed appendage. However, a distinct swollen region occurs upon the stylar shaft of *Haplophyton* just below the papillose cap, which might be regarded as a primitive stage in the development of the more elaborate appendage of *Amsonia. Rhazya* is also a genus closely related to *Amsonia,* but possesses a disc and a jointed clavuncle among other dissimilarities.

Relationship and Distribution of the Subgenera

The genus *Amsonia,* although relatively a small group, is readily separable into three subgenera, which, while interlocking closely, are distinct and well differentiated entities in the whole. The series of subgenera range in geographical and evolutionary succession from east to west and south in North America, upon which continent the bulk of the species occur, only one species being found in eastern Asia.

The subgenus *Euamsonia* is the largest of the divisions in number of species and varieties and the most widely spread, embracing five species and four varieties in the southeastern United States, and one species in Japan. The second largest

[1] Gray, Syn. Fl. N. Am. 2[1]: 81. 1878.

subgenus with regard to number of species and extent of distribution is *Sphinctosiphon*, which occurs with eight species in the central-southwestern United States and adjacent Mexico, having for its center of distribution southern New Mexico and northern Chihuahua. *Articularia* is the smallest of the subgenera, and contains four species limited to southern California, southern Nevada, southwestern Utah, and western Arizona; while one species, *A. arenaria*, is isolated from the general distribution of the subgenus to which it belongs, in extreme southwestern New Mexico and adjoining Chihuahua.

The situation of *Euamsonia* in having species of the southeastern United States and Japan is by this time of more or less frequent knowledge, and no speculations will be devoted to it, since similar instances have been reported.[1, 2, etc.]. The occurrence of the three subgenera in the southern United States and northern Mexico is, however, of general interest.

A study of the genus in North America suggests forcibly that it is a genus of mesophytic origin which exhibits an increasing adaptation to an arid habitat. *Euamsonia* is the one subgenus of a mesophytic habit, and since it is represented by the relict species in Japan to which reference has already been made, it is taken as the most primitive. The subgenera *Sphinctosiphon* and *Articularia* are plants of distinctly arid habitat, and the morphological differentiation which those groups exhibit are interpreted as divergences from the primitive condition represented by *Euamsonia*.

The genus *Amsonia* is relatively advanced among the Plumeroideae because of its highly differentiated stigmatic-cap, among other characters, and it is upon the basis of further differentiation in that respect that the first subgeneric division is made. In the subgenus *Euamsonia* the stigma proper is depressed-capitate or truncate, and appears merely as the freer summit of the papillose central region of the stigmatic-cap to which reference was made in detail in the previous section concerning Gross Morphology. The mouth of the corolla-tube, moreover, is relatively open, continuing the dilation of the tube. In the

[1] Gray, A. Mem. Am. Acad. N. S. **6**: 377–449. 1859.
[2] Fernald, M. L. Quart. Rev. Biol. **1**: 227. 1926.

subgenus *Sphinctosiphon* an evolutionary advance is detected in the elevation of the stigma to the position of two distinct apiculate lobes, and the constriction of the mouth of the corolla-tube. Such differentiations are obviously of use to the plant for insect pollination in an arid region.

The subgenus *Articularia* demonstrates a further advance in the articulation of the follicles, which are quite slender and continuous in *Euamsonia* and *Sphinctosiphon*, into thickish constricted segments in much the same manner as the legumes of certain desert Leguminosae, beside having the apiculate characters of the stigma. The seeds of the follicles of *Articularia*, moreover, are larger and ovoid, and the endosperm is thickened, but of a light and corky texture, an evident construction to facilitate easy dissemination in an arid habitat. The seeds of *Euamsonia* and *Sphinctosiphon*, on the other hand, are roughly cylindrical with a relatively thin, hard endosperm.

The subgenera of *Amsonia* are remarkable for their interrupted distribution, a factor which lends even sharper distinction to the morphological differences which they display, and suggests certain hypotheses for their origin. *Euamsonia*, with the greatest number of species and varieties, has been found naturally in all of the southeastern United States, with a generally characteristic habitat of moist woods, ravines, or streamsides, save in its extreme western limits, where *A. ciliata* var. *texana* is found on rocky hillsides and prairies.

Sphinctosiphon, with the next largest number of species, is confined to southwestern Colorado, southeastern Utah, New Mexico, and adjacent portions of Arizona, Chihuahua, and Texas. Thus *Sphinctosiphon* and *Euamsonia* are entirely separate in range, except in south-central Texas, which contains two species of *Euamsonia* and a limited colony of *A. salpignantha* of *Sphinctosiphon*. Besides the anomalous occurrence of *A. salpignantha* within the southwestern limits of *Euamsonia* the nearest that the subgenera approach each other is evidently in western Texas, *Euamsonia* being found in the Wichita Mountains of north-central Texas, and *Sphinctosiphon* in the Guadaloupe Mountains about two hundred miles to the southwest. The species of *Sphinctosiphon*, although in an arid region,

partake of the nature of *Euamsonia* in frequenting the borders of ponds, streams, and branches.

Articularia, with the fewest number of species, is confined to southern California, southern Nevada, southwestern Utah, and northwestern Arizona, save for the species *A. arenaria,* which has a distribution analogous to the anomalous distribution of *A. salpignantha* of *Sphinctosiphon,* occurring separate from the other species with which it has its affinities, in extreme southwestern New Mexico (Grant County), and adjacent Chihuahua, within the distributional area of *Sphinctosiphon.* The species of *Articularia* demonstrate the most extreme endurance for aridity, being found most frequently in the sand of the open desert, whence, it is rather safely supposed, occurs the striking morphological adaptations which they exhibit.

Thus *Sphinctosiphon* and *Articularia* possess rather distinct areas of distribution, save for *A. arenaria* of *Articularia* which occurs fully three hundred miles, to present knowledge, from the known range of its kindred species, a perplexing situation. It is also possible that *A. Eastwoodiana* and *A. Jonesii,* species of *Articularia* and *Sphinctosiphon* respectively, meet in southern Utah and northern Arizona. At any rate, *A. Kearneyana,* occurring in regions midway between the territories of *Sphinctosiphon* and *Articularia,* for reasons which will be advanced later, appears in all probability an hybrid between *A. Palmeri* of the former subgenus and *A. brevifolia* of the latter. Thus it is seen that the subgenera of *Amsonia* occupy essentially distinct and isolated ranges, *Articularia* and *Sphinctosiphon,* the most nearly related of the groups morphologically and ecologically, being also the most neighborly distributed, and both distinctly removed from *Euamsonia,* the supposed primitive subgenus, morphologically and geographically.

If we are to believe that by the Cretaceous the modern angiospermous type of vegetation had become fully established throughout the world,[1] we may assume that the genus *Amsonia* was by that time in a flourishing condition with a wide distribution over the southern half of what is now the United States

[1] Grabau, A. W. Textbook of geology **2:** 687. 1922.

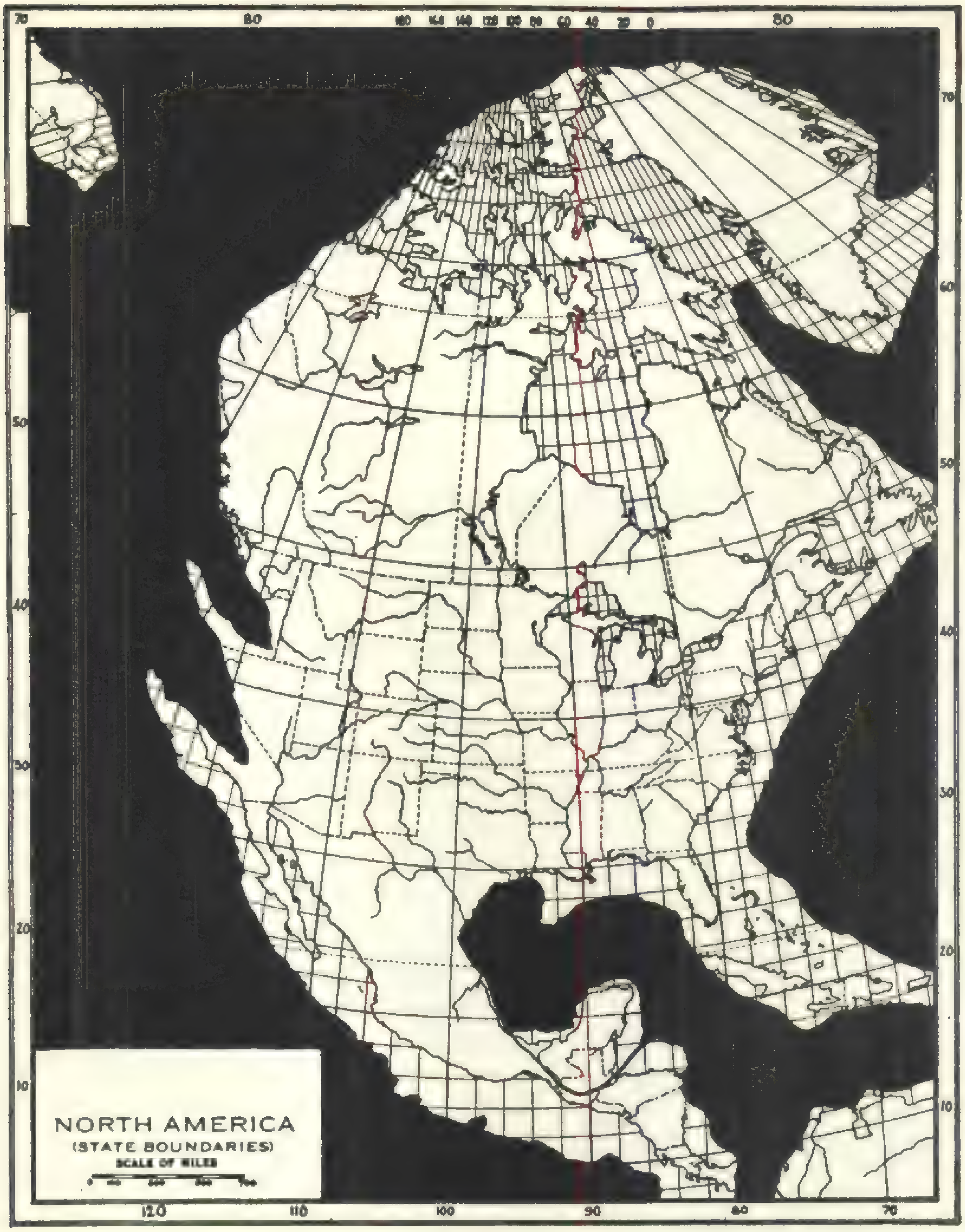

Fig. 1. Land mass of North America in Comanchean time.

and adjacent Mexico.[1] The position of the land masses in

[1] Stopes, M. C. Ancient plants, p. 85. 1910. Dr. Stopes wrote, in support of such an assumption: "Specimens of Cretaceous plants from various parts of the world seem to indicate that there was a striking uniformity in the flora of that period all over the globe."

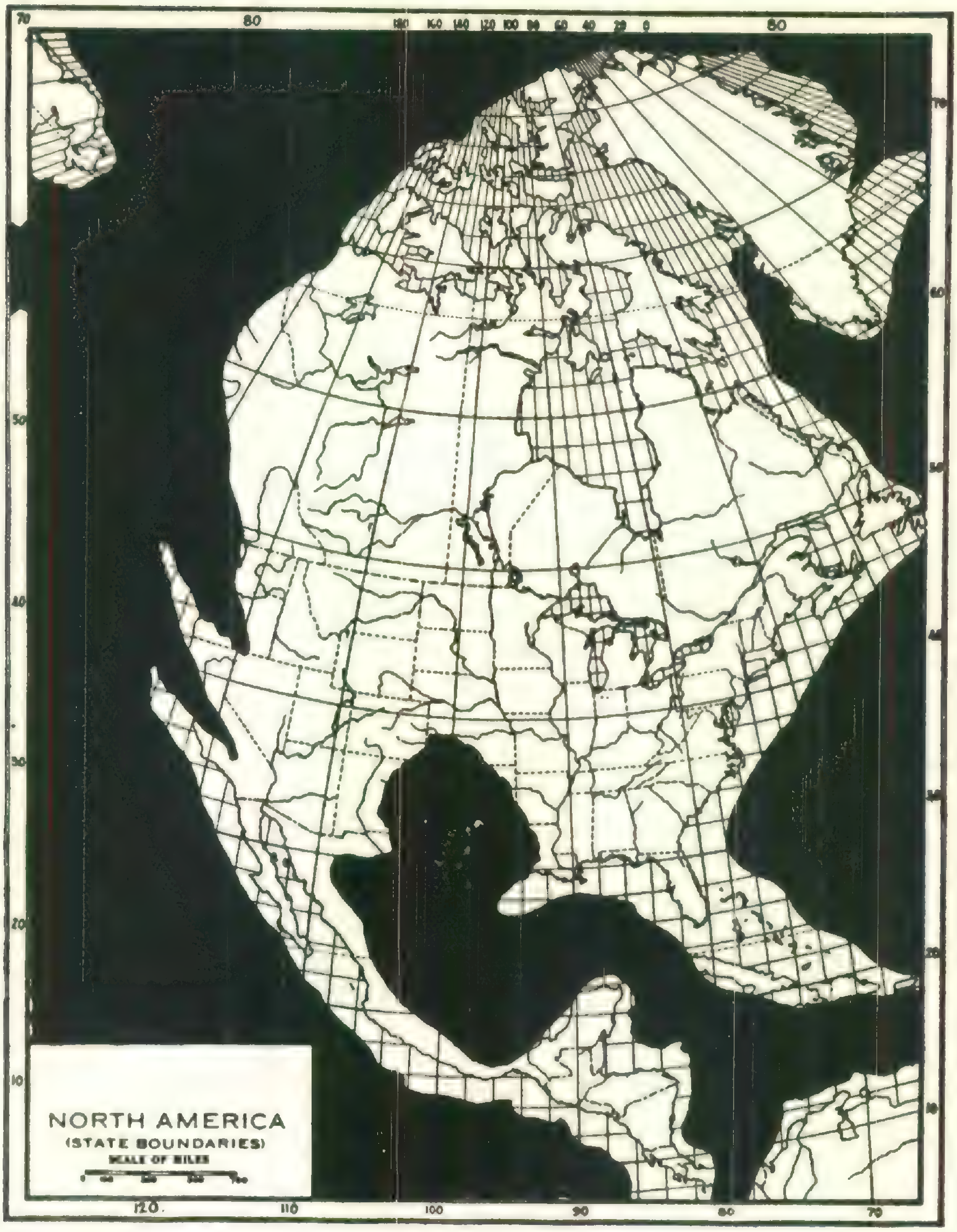

Fig. 2. Land mass of North America in late Comanchean time.

Comanchean, or lower Cretaceous, time would lend support to the speculation that the genus was allowed at that time practically an uninterrupted range (fig. 1), and because of that reason was very likely of a more or less uniform character. The

fact that the genus is now found as a relict in Japan is reason enough for assuming a wide range for its species.

During the late Comanchean time, however, the continuous range supposed for the genus was broken by the inundations of the Colorado Trough (fig. 2), which occurred over nearly the whole of northeastern Mexico, Texas, and parts of Oklahoma, Colorado, Kansas, and New Mexico. This invading sea could scarcely be regarded as less than a most effective opportunity for generic variation through isolation, especially since the vegetation in the isolated mass was by that time bearing evidence of an adaptation to aridity.[1]

The Cretaceous time, proper, is well known for the extensive inundations which then occurred widely in North America, and the break in the hypothetical distribution of *Amsonia* was heightened by an increase of the seas of the Colorado Trough, which cut completely through the continent from what is now the coast of the Territory of Mackenzie to the Gulf of Mexico. Troughs of the western coast also caused intrusions during the early periods of the Cenozoic, reaching a climax during Miocene time, when large tracts of southern California and adjacent Lower California and Arizona were separated as islands (fig. 3). By the Pliocene time, North America had largely assumed the shape with which we are now familiar.

With isolated land masses corresponding roughly to the localities of probable origin of the subgenera *Sphinctosiphon* and *Articularia*, a fair degree of credence might be allowed the assumption of their differentiation upon those lands, the first instance of isolation, the intrusion of the Colorado Trough, possibly giving rise to the development of the type of *Sphinctosiphon* from the primitive condition represented at present by *Euamsonia*, and the second, the production of islands by the inundations of the west coast troughs during the Miocene, providing an opportunity for the divergence of the type of *Articularia* from the group now represented by *Sphinctosiphon*. It is

[1] Schuchert, C. Outlines of historical geology. 1924. "In general we may say that after the early upper Cretaceous time . . . the climate the world over was . . . warm temperate in character [p. 612.] With the Miocene, however . . . more or less of desert climates developed in the Cordilleran areas of North America and have prevailed there ever since [p. 626]."

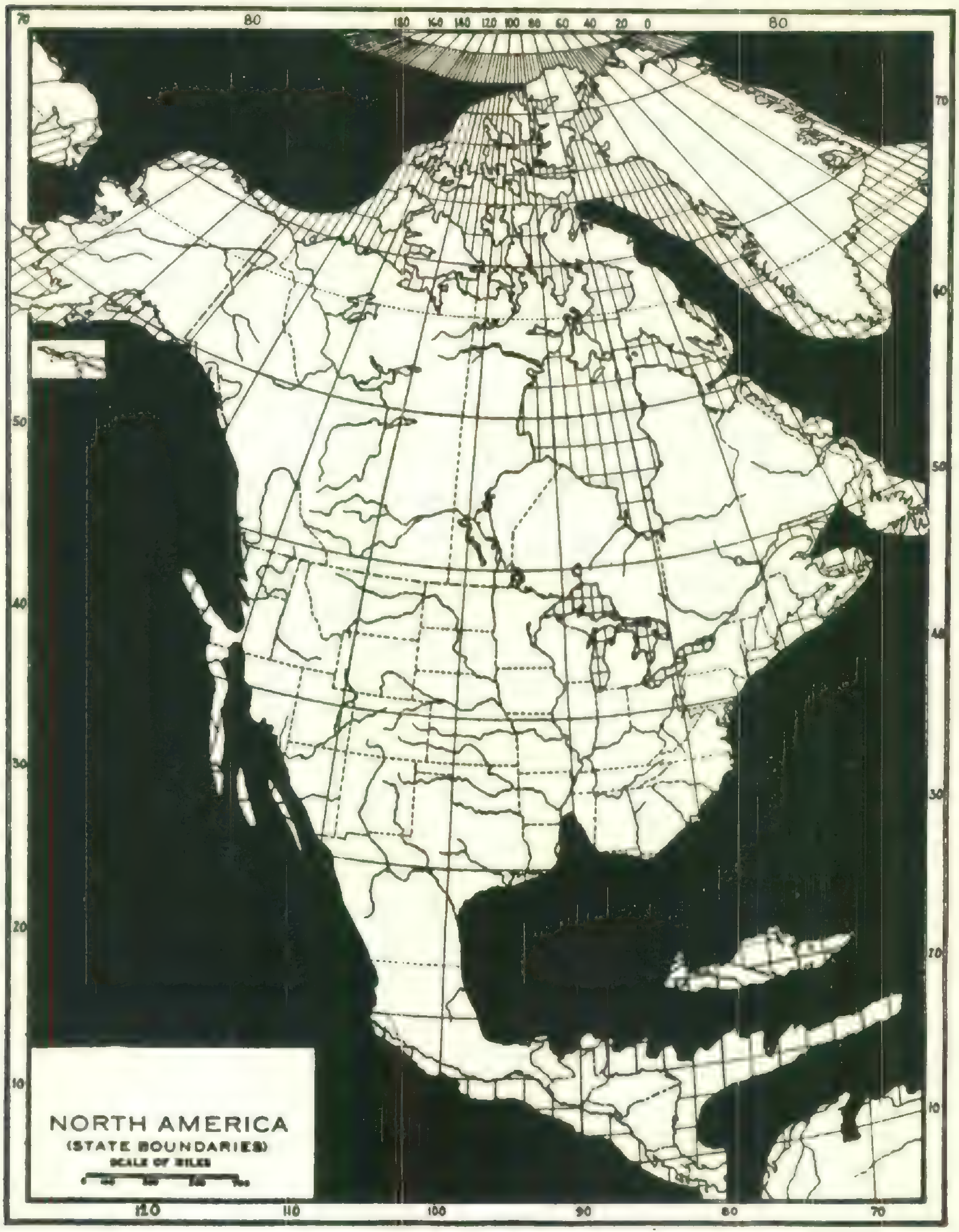

Fig. 3. Land mass of North America in upper Cretaceous time.

believed that the discontinuous areas of the subgenera support the hypothesis offered for their origin. The fact that the distribution of the three subgenera still bears evidence of disruption thousands of years after the Mesozoic and Cenozoic inundations appears quite striking, and bears additional evidence of

the old age[1] of the genus in its inability to reunite its former distribution. In this respect, the genus *Amsonia* offers an interesting parallel to the endemics of the unglaciated regions of boreal America, whose ranges were broken by the Pleistocene glacial phenomena: "These older species in North America have long since passed their period of aggressiveness. 'Left undisturbed they persist in their old habitats, but they fail to move into new and immediately neighboring territory.'"[2]

Abbreviations

Abbreviations indicating the herbaria where specimens cited in this monograph are deposited are as follows:

Baker = C. F. Baker Herbarium of Pomona College.
F = Field Museum of Natural History Herbarium.
G = Gray Herbarium of Harvard University.
MBG = Missouri Botanical Garden Herbarium.
NE = New England Botanical Club Herbarium.
NY = New York Botanical Garden Herbarium.
P = Pomona College Herbarium.
ANSP = Academy of Natural Sciences of Philadelphia Herbarium.
PBC = Philadelphia Botanical Club Herbarium.

TAXONOMY

Amsonia Walt. Fl. Carol. 98. 1788; Michx. Fl. Bor. Am. **1**: 121. 1803; Pursh, Fl. Am. Sept. ed. 1, **1**: 184. 1814; Roem. & Schult. Syst. Veg. **4**: 432. 1819; Smith in Rees, Cycl. **35**: end of art. "Tabernaemontana." 1819; Elliott, Sketch Bot. S. C. & Ga. 316. 1821; Endl. Gen. Pl. 582. 1838; A. DC. in DC. Prodr. **8**: 384. 1844; Pfeiffer, Nom. Bot. **1**^{1}: 156. 1873; Benth. & Hook. Gen. Pl. **2**: 703. 1876; Gray, Syn. Fl. N. Am. **2**^{1}: 81. 1878; Durand, Index Gen. Phan. 262. 1888; Baill. Hist. Pl. **10**: 180. 1891; Coulter, Contr. U. S. Nat. Herb. **2**: 262. 1892; Coville, Contr. U. S. Nat. Herb. **4**: 142. 1893;

[1] The presence of *Amsonia* in the Cretaceous period would give to the genus an age, based upon the most capable of present calculations (Schuchert, C. *l. c.* 485. 1924), of at least 45,000,000 years.

[2] Fernald, M. L. Persistence of plants in unglaciated areas of boreal America. Mem. Am. Acad. **15**: 244. 1925; Antiquity of vascular plants. Quart. Rev. Biol. **1**: 227. 1926.

K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. **4**[2]: 143. 1895; Mohr, Contr. U. S. Nat. Herb. **6**: 674. 1901; Small, Fl. Southeast. U. S. 934. 1903; Dalla Torre & Harms, Gen. Siph. 406. 1904; Harper, Ann. N. Y. Acad. Sci. **17**[1]: 175. 1906; Robinson & Fernald in Gray, New Man. ed. 7, 661. 1908; Nelson in Coulter & Nelson, New Man. Rocky Mt. Bot. 385. 1909; Matsumura, Index Pl. Jap. **2**: 505. 1912; Wooton & Standley, Contr. U. S. Nat. Herb. **19**: 504. 1915; Rydb. Fl. Rocky Mts. 668. 1917; Davidson & Moxley, Fl. South. Cal. 278. 1923; Tidestrom, Contr. U. S. Nat. Herb. **25**: 418. 1925; Jepson, Man. Fl. Pl. Cal. 768. 1925.

Ansonia Raf. New Fl. N. Am. **4**: 58. 1838.

Lactescent herbaceous caulescent perennials, glabrous or pubescent. Leaves alternate or subverticillate, sessile or petiolate, membranaceous or somewhat thickened and fleshy, entire. Inflorescence a terminal thyrsoid or corymbose cyme. Calyx five-parted, the lobes acuminate or subulate. Corolla salverform, villous within, tube cylindrical, dilating, open or constricted; lobes ovate to lanceolate, spreading or nearly erect. Stamens five, adnate to the corolla-tube above the middle, included; anthers ovate to ovate-lanceolate, obtuse, unappendaged. Disk wanting. Carpels two, united by the filiform style surmounted by a truncate stigmatic-cap. Stigma depressed-capitate, or apiculate by two distinct lobes, surrounded by a spherical papillose mass, and appendaged by a reflexed membrane. Ovules in each carpel many, two-seriate. Follicles two, cylindrical, continuous or articulated. Seeds many, oneseriate, cylindrical, unappendaged. Embryo straight.

Type species: *A. Tabernaemontana* Walt. Fl. Carol. 98. 1788.

Synopsis of the Subgenera and Sections

KEY TO THE SUBGENERA

A. Stigma depressed-capitate or truncate...............Subgenus I. Euamsonia
B. Stigma apiculate by two distinct lobes.
  a. Follicles continuous, not articulated..........Subgenus II. Sphinctosiphon
  b. Follicles torose, articulated into thickish constricted segments.......
  ....Subgenus III. Articularia

Subgenus I. Euamsonia (K. Schumann) Woodson

Subgenus I. Euamsonia (K. Schumann) Woodson, n. comb.

§*Euamsonia* K. Schumann in Engl. & Prantl, Nat. Pflanzen-

fam. 4[2]: 143. 1895; Dalla Torre & Harms, Gen. Siph. 406. 1904.

Bracteoles inconspicuous; orifice of the corolla-tube not constricted in anthesis; stigma depressed-capitate or truncate; follicles slender and continuous, not articulate, fibrous, not horny in texture; seeds irregularly oblong in outline, truncate at either end, variously pitted and wrinkled; plants of the southeastern United States and Japan. Spp. 1–5.

KEY TO THE SPECIES AND VARIETIES

a. Corolla glabrous without.
  b. Leaf-blades elliptic, distinctly petiolate throughout..........*1. A. rigida*
  bb. Leaf-blades oblong-lanceolate to linear, sessile or subsessile above.
    c. Corolla-tube 6–8 mm. long.
      d. Stem-leaves 4–15 times as long as broad; inflorescence barely held above the foliage........................*2. A. ciliata*
      dd. Stem-leaves 15–30 times as long as broad; inflorescence held high above the foliage..........*2a. A. ciliata* var. *tenuifolium*
    cc. Corolla-tube 9–12 mm. long.
      d. Corolla-lobes about half as long as the tube; pedicels 3–5 mm. long; species of North America..*2b. A. ciliata* var. *texana*
      dd. Corolla-lobes about equalling the tube; pedicels 5–10 mm. long; species of Asia........................*3. A. elliptica*
aa. Corolla pubescent without.
  b. Follicles glabrous.
    c. Leaf-blades ovate to oblong-lanceolate, the bases of the lower obtuse to broadly acute..................*4. A. Tabernaemontana*
    cc. Leaf-blades lanceolate to linear-lanceolate, the bases of the lower acute to acuminate.
      d. Inflorescence loose, few-flowered; foliage glabrous, glaucous beneath...............*4a. A. Tabernaemontana* var. *salicifolia*
      dd. Inflorescence dense, many-flowered; foliage pubescent, glabrate in age..........*4b. A. Tabernaemontana* var. *Gattingeri*
  bb. Follicles pubescent, at least upon the upper portion.......*5. A. ludoviciana*

1. **Amsonia rigida** Shuttlew. in Small, Fl. Southeast. U. S. 935. 1903; Harper, Ann. N. Y. Acad. Sci. **17**[1]: 175. 1906. Pl. 51, figs. 4–6.

Herbaceous perennial from a thickened somewhat woody root; stems 8–15 dm. tall, regularly branched above, glabrous; leaves alternate, numerous, the blades almost exactly elliptic, isophyllous, *i. e.*, the lower and the upper leaves of nearly like outline, green above, glaucous or glaucescent beneath, 2.5–6 cm. long, .5–1.5 cm. broad, distinctly petiolate throughout; flowers rela-

tively numerous in fairly loose cymes; pedicels 5 mm. long or slightly less; calyx 1–1.5 mm. long, glabrous, the lobes triangular-ovate; corolla salverform, the tube 6–8 mm. long, gradually dilating upwards, glabrous without, the lobes lanceolate, 7–10 mm. long, widely spreading; stigmatic-cap about as tall as broad, stigma depressed-capitate; follicles slender, continuous, gradually attenuate, 7–11 cm. long, sessile, glabrous, 7–10-seeded; seeds 5–11 mm. long, oblong in outline, truncate at either end, variously wrinkled and pitted, dark brown.

Distribution: swampy or moist pine forests, northern Florida and southern Georgia.

Specimens examined:

GEORGIA: Alapaha, swampy pine woods, June 25, 1901, *Curtiss 6820* (G, MBG, NY, US); Sumter Co., moist pine barrens, Aug. 21, 1900, *Harper 448* (G, MBG, NY, US, F); same locality, Sept. 6, 1900, *Harper 606* (NY, US); same locality, Aug. 21, 1900, *Harper 440* (NY, US).

FLORIDA: Chattahoochee, May, 1882, *Curtiss* (G); data lacking, *Chapman* (G, ANSP, MBG); St. Marks, June, 1843, *Rugel* (MBG); Chattahoochee, 1891, *Chapman* (MBG).

2. Amsonia ciliata Walt. Fl. Carol. 98. 1788; A. DC. in DC. Prodr. **8**: 385. 1844; Wood, Classbook Bot. 589. 1860; Chapm. Fl. South. U. S. 343. 1897; Mohr, Contr. U. S. Nat. Herb. **6**: 674. 1901; Small, Fl. Southeast. U. S. 935. 1903; Harper, Ann. N. Y. Acad. Sci. **17**^{1}: 175. 1906. Pl. 51, figs. 7–8.

Tabernaemontana angustifolia Ait. Hort. Kew. **1**: 300. 1789; Willd. Sp. Pl. **1**^{2}: 1247. 1798.

Amsonia angustifolia (Ait.) Michx. Fl. Bor. Am. **1**: 121. 1803; Pursh, Fl. Am. Sept. ed. 1, **1**: 184. 1814; Roem. & Schult. Syst. Veg. **4**: 432. 1819; Ell. Sketch Bot. S. C. & Ga. 317. 1821; Darby, Bot. South. States, 434. 1860; Gray, Syn. Fl. N. Am. **2**^{1}: 81. 1878.

Ansonia ciliata (Walt.) Raf. New Fl. N. Am. **4**: 58. 1838.

Ansonia angustifolia (Ait.) Raf. *l. c.* 1838.

Herbaceous perennial from a thickened woody root; stems 7–15 dm. tall, clustered from the base, erect or slightly ascending, sparsely branched above, the branches ascending, pubes-

cent, glabrous or glabrate in age; leaves numerous, crowded, subverticillate above, slightly heterophyllous, *i. e.*, the lower leaves broader and of a slightly different outline than the upper, linear-lanceolate, or the lower oblong-lanceolate, pubescent, or glabrate in age; inflorescence dense, barely held above the foliage; pedicels 3–5 mm. long, sparsely pubescent; calyx 1–1.5 mm. long, glabrous, or with a few scattered hairs, the lobes triangular-ovate; corolla salverform, the tube 6–8 mm. long, glabrous without, the lobes 7–8 mm. long, oblong-lanceolate, erect or spreading; stigmatic-cap slightly broader than tall, stigma depressed-capitate or truncate; follicles slender, continuous, 9–11 cm. long, gradually attenuate, sessile, glabrous, 7–11-seeded; seeds 5–11 mm. long, oblong in outline, truncate at either end, variously pitted or wrinkled, dark brown.

Distribution: pine forests, occasionally entering fields; North Carolina, South Carolina, southern Georgia, northern Florida, southern Alabama, and northeastern Texas.

Specimens examined:

North Carolina: data lacking, *Curtis* (G).

South Carolina: Aiken, April, 1882, *Velden* (MBG); Aiken, sand hills near Graniteville, May 7, 1899, *Eggert* (MBG); Aiken, May, 1869, *Canby 68* (MBG, G, NY); Columbia, woods, May 9, 1899, *Sargent* (G); data lacking, *Ravenel* (G, NY, US); Columbia, dry sandy pine woods, May, 1890, *Taylor* (F).

Georgia: Richmond Co., slopes of sand hills about 8 miles west of Augusta, June 10, 1902, *Harper 1319* (US, NY, F); Augusta, date lacking, *Olney & Metcalfe 76* (G); data lacking, *Wilkins* (G).

Florida: Tallahassee, date lacking, *Berg* (NY); Aspalaga, dry pine woods, April, year lacking, *Curtiss 2269* (G, MBG, ANSP, US, F); River Junction, fields and open woods, April 22 and May 16, 1898, *Curtiss 6376* (G, NY, US, MBG); data lacking, *Chapman* (G); Aspalaga, May, 1898, *Chapman* (MBG); Coffee Co., rocky open ground, flood plains of Pea River, May 15, 1925, *E. J. Palmer 27233* (MBG); Chehaw, June 24, 1915, *Drushel 4572* (MBG).

Alabama: data lacking, *Durand* (ANSP).

Texas: San Marcos, June 6, 1897, *Stanfield* (NY); Mid-

lothian, April 30, 1895, *Plank* (NY); Turtle Creek, Kerr Co., date lacking, *Bray 239* (US); Orange, April 17, 1899, *Bray 60* (US).

Although recognizing that *A. ciliata* Walt. antedates *A. angustifolia* (Ait.) Michx., Gray placed Walter's species in synonymy with the latter species, remarking that *ciliata* was an inappropriate name. The specimens with Gray's labels in the Gray Herbarium truly are glabrate or glabrous, being overly matured specimens, hence Dr. Gray's impression. In any event, Walter's name can scarcely be discarded.

2a. Var. **tenuifolia** (Raf.) Woodson, n. comb.

Ansonia tenuifolia Raf. New Fl. N. Am. **4**: 58. 1838.

Amsonia salicifolia Pursh var. *ciliolata* A. DC. in DC. Prodr. **8**: 384. 1844.

Amsonia ciliata Walt. var. *filifolia* Wood, Classbook Bot. 589. 1860.

Amsonia tenuifolia (Raf.) Harper, Ann. N. Y. Acad. Sci. **17**[1]: 175. 1906.

Herbaceous perennial from a fibrous root; stems 3–10 dm. tall, single or sparingly clustered from the base, erect or slightly ascending, sparingly branched above, the branches ascending, pubescent or glabrate in age; leaves numerous, crowded, subverticillate, scarcely heterophyllous, *i. e.*, the lower leaves barely broader and of about the same outline as the upper, linear-lanceolate to filiform, pubescent or glabrate; inflorescence dense, held high above the foliage by a slender, usually leafless stalk; pedicels 3–5 mm. long, barely strigose or glabrous; calyx 1–2 mm. long, glabrous, or with a few short hairs, the lobes triangular-attenuate; corolla salverform, the tube 6–8 mm. long, glabrous or slightly canescent without, the lobes 4–6 mm. long, ovate to oblong-lanceolate, erect or spreading; stigmatic-cap about as tall as broad, stigma depressed-capitate or truncate; follicles slender, continuous, 8–14 cm. long; seeds 7–12 mm. long, oblong in outline, truncate at either end, variously pitted or wrinkled, brown.

Distribution: sand-hills and barrens, also rocky margins of streams; North Carolina, South Carolina, Georgia, Florida, Ala-

bama, southern Arkansas, Missouri, Texas, and central Mexico.

Specimens examined:

UNITED STATES:

NORTH CAROLINA: data lacking, *Curtis* (G); White Hall, May 13, 1896, *Biltmore 1400* (US).

SOUTH CAROLINA: Aiken, May 21, 1899, *Eggert* (MBG).

GEORGIA: Altamaha, sand-hills, date lacking, *Chapman* (G); Augusta, sand-hills, June 10, 1902, *Harper 1319* (G, MBG, NY); Bainbridge, low woods bordering Flint River, July 13, 1899, *Curtiss 6476* (G, MBG, NY, US); Bulloch Co., sand-hills along Big Lott's Creek, June 17, 1901, *Harper 915* (G, MBG, NY, US, F); Camilla, Mitchell Co., dry sand barrens, Aug. 7, *Harper 1166* (G, NY, US); Dublin, Laurens Co., sand-hills of Oconee River, April 20, 1904, *Harper 2138* (G, MBG, NY, US, F); Jasper City, 1846–48, *Porter* (G); Dooly Co., dry pine barrens near Gum Creek, Sept. 3, 1900, *Harper 577* (US); Burke Co., Aug. 15, 1897, *Hopkins 83* (NY); Thomson, McDuffie Co., sand-hills, Sept. 9, year lacking *Bartlett 1493* (P); Vidalia, April, 1914, *Huger* (MBG); Macon, date lacking, *Green* (ANSP).

FLORIDA: Bellair, Sept. 3, 1895, *Nash 2546* (G, MBG, US, F); Clarcona, Orange Co., date lacking, *Meislahn 210* (US); Gotha, March 28, 1919, *Nehrling 12* (US); pine woods west of Jacksonville, April, 1848, *Rugel 21* (US, MBG, F, NY); data lacking, 1873, *Fell* (ANSP); Cocoanut Grove, 1899, *Rodman* (G); Sumter Co., grassy pine-barrens, March 11, 1883, *Donnell-Smith* (G); "East Florida," date lacking, *Buckley* (G); "Middle Florida," date lacking, *Eaton* (G); data lacking, *Buckley* (G); Alachua Co., June–July, 1898, *Hitchcock* (MBG); Lake Brantley, Aug. 1, 1895, *Williamson* (ANSP).

ALABAMA: data lacking, *Buckley* (MBG); Bon Secour (near Mobile), June 29, 1893, *Mohr* (US).

MISSOURI: Ozark Co., rocky open ground, bald knobs, near Tecumseh, Oct. 9, 1927, *E. J. Palmer 33031* (MBG); summit of bald knob across river from Tecumseh, Ozark Co., Nov. 11, 1928, *Anderson & Woodson 4000* (MBG).

ARKANSAS: Logan Co., rocky margins of small streams, Oct. 18, 1923, *E. J. Palmer 24203* (G); Hot Springs, Aug. 5, 1879, *Letterman* (MBG); Arkadelphia, May 10, 1884, *Letterman* (MBG).

Texas: data lacking, *Wright* (G); Medina Lake, Bandera Co., limestone ledges, creek banks, June 14, 1917, *E. J. Palmer 12262* (MBG); Johnson Co., rocky prairies, April, 1882, *Reverchon 84* (MBG).

Mexico:

Michoacan: Morelia, June, 1901, *Arsène* (F).

2b. Var. **texana** (Gray) Coulter, Contr. U. S. Nat. Herb. **2:** 262. 1892.

Amsonia angustifolia Michx. var. *Texana* Gray, Syn. Fl. N. Am. **2**[1]**:** 81. 1878.

Amsonia texana (Gray) Heller, Muhlenbergia **1:** 2. 1900; Small, Fl. Southeast. U. S. 935. 1903; Rydb. Fl. Colo. 269. 1906; Nelson in Coulter & Nelson, New Man. Rocky Mt. Bot. 385. 1909; Clem. & Clem. Rocky Mt. Fl. 100. 1914.

Herbaceous perennial from a slightly woody root; stems 2–5 dm. tall, usually clustered from the base, erect or slightly ascending or spreading, occasionally pubescent when young, mostly glabrous; leaves alternate, numerous, quite heterophyllous, *i. e.*, the lower leaves broader and of a different outline than the upper, ovate to oblong-lanceolate below, lanceolate to linear-lanceolate above, occasionally with short scattered hairs; inflorescence compact, barely held above the foliage; pedicels 3–5 mm. long; calyx 1.5–2.5 mm. long, glabrous or glabrate, the lobes triangular-lanceolate to subulate; corolla salverform, the tube 9–11 mm. long, glabrous without, the lobes 4–6 mm. long, ovate to ovate-lanceolate, spreading; stigmatic-cap broader than tall, stigma truncate; follicles slender, continuous, 6–10 cm. long, rather abruptly acuminate, sessile, glabrous 5–15-seeded; seeds 5–11 mm. long, oblong in outline, truncate at the ends, variously pitted or wrinkled, brown.

Distribution: dry and rocky hillsides and prairies; Oklahoma, and Texas.

Specimens examined:

Oklahoma: Crusher Spur, Murray Co., rocky mountain-side, April 12, 1913, *Stevens 29* (G, MBG, US); Fort Sill, May 20, 1892, *Sydone* (NY); Tishomingo, on hillsides, common, April 8, 1916, *Houghton 3606* (G); vicinity of Fort Sill, April 12, 1916,

Clemens 11727 (MBG); Cache, Comanche Co., dry hillsides, decomposed granite, July 19, 1917, *E. J. Palmer 12597* (MBG); Davis, Arbuckle Mts., April 1, 1916, *Emig 399* (MBG).

TEXAS: Comanche Springs, March, 1849, *Lindheimer* (G, MBG); Dallas, rocky prairies, April, 1875, *Reverchon* (G, NY, MBG); Dallas, dry uplands, March–June, year lacking, *Reverchon* (G, MBG); "Upper Colorado," rocky places, 1847, *Lindheimer 660* (G TYPE, MBG, US, F); Fort Worth, rocky hillsides, May 7, 1911, *Ruth 241* (G, NY, ANSP, F); "Witicha Mtns.," July, 1852, *Torrey* (G, NY); data lacking, *Lindheimer* (ANSP, MBG); Dallas, dry soil, April–June, 1877, *Reverchon 598* (US, MBG); Dallas, common in woods, May 7, 1900, *Bush 646* (US, NY, MBG); Dallas, rocky prairies, June 30, 1877, *Hall 515* (US, MBG, NY); Forks, May 27, year lacking, *Reverchon* (MBG); Boerne, Kendall Co., low rocky creek banks, April 6, 1917, *E. J. Palmer 11471* (MBG); Dallas, rocky hills, West Dallas, June 22, 1899, *Eggert* (MBG); Hood Co., prairies, May 4, 1900, *Eggert* (MBG); Dallas, cement works, April 12, 1902, *Reverchon* (MBG); data lacking, *Lindheimer 4* (MBG); Gillespie Co., date lacking, *Jermy 145* (MBG); Dallas, open limestone hills, May 4, 1918, *E. J. Palmer 13496* (MBG); Lacey's Ranch, Kerr Co., moist rocky creek banks, June 11, 1917, *E. J. Palmer 12233* (MBG); Bull Creek, near Austin, April 11, 1914, *Young* (MBG); Boerne, Kendall Co., moist rocky creek banks, April 20, 1917, *E. J. Palmer 11616* (MBG); Dallas, high prairies, April 12, 1902, *Reverchon 3122* (MBG).

3. **Amsonia elliptica** (Thunb.) Roem. & Schult. Syst. Veg. **4:** 432. 1819; A. DC. in DC. Prodr. **8:** 384. 1844; Franch. & Savatier, Enum. Pl. Jap. **1:** 315. 1874; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**^{2}**:** 143. 1895; Matsumura, Index Pl. Jap. **2:** 505. 1912. Pl. 51, figs. 9–10.

Tabernaemontana elliptica Thunb. Fl. Jap. 111. 1784.

Ansonia elliptica (Thunb.) Raf. New Fl. N. Am. 4: 58. 1838.

"*Amsonia elliptica* Sieb. & Zucc." in Gray, Mem. Am. Acad. **6:** 403. 1857.

Herbaceous perennial from a slightly thickened root; stems 4–7 dm. tall, single or clustered from the base, erect or slightly

ascending, glabrous, or very slightly pubescent when young, branched above, the branches ascending or somewhat spreading; leaves alternate, relatively distant, the blades relatively narrow, lanceolate to linear-lanceolate, the lower 5–10 times as long as broad, both the bases and the apices narrowly acute to acuminate, glabrous above, glaucescent beneath, becoming green in age; inflorescence loose, relatively few-flowered, pedicels 5–10 mm. long; calyx 1–2 mm. long, the lobes triangular-lanceolate, glabrous; corolla salverform, the tube relatively broad, 10–12 mm. long, glabrous without; the lobes of about equal length, oblong-lanceolate, spreading; stigmatic-cap about as broad as tall, stigma depressed-capitate or truncate; follicles relatively stout, continuous, or very slightly torose, 4–6 cm. long, sessile, glabrous, 5–10-seeded; seeds 5–10 mm. long, oblong in outline, truncate at either end, variously pitted or wrinkled, brown.

Distribution: northern Japanese Archipelago.

Specimens examined:

JAPAN: Hakodate, 1861, *Maximowicz* (G); Jesso, near Hakodate, 1861, *Albrecht* (G); Todahara, Musashi, May 24, 1891, *Watanabe* (G); Tokio, May 7, 1879, *Matsumura* (US); Musaski, Toda, May 27, 1911, collector lacking (US).

4. Amsonia Tabernaemontana Walt. Fl. Carol. 98. 1788; Pers. Syn. **1**: 269. 1801; A. DC. in DC. Prodr. **8**: 384. 1844; Rept. Torr. Bot. Mex. Bound. Surv. 159. 1859; Gray, Syn. Fl. N. Am. **2**[1]: 81. 1878; Wood, Classbook Bot. 589. 1860; Gattinger, Tenn. Fl. 63. 1887; Coulter, Contr. U. S. Nat. Herb. **2**: 262. 1892; K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. **4**[2]: 143. 1895; Chapm. Fl. South. U. S. 343. 1897; Robinson & Fernald in Gray, New Man. ed. 7, 661. 1908.

Pl. 51, figs. 11–13.

Anonymus suffrutex Gronov. Fl. Virg. ed. 2, 35. 1762.

Tabernaemontana Amsonia L. Sp. Pl. ed. 2, **2**: 301. 1762; Willd. Sp. Pl. **1**[2]: 1246. 1798.

Tabernaemontana humilis Salisb. Prodr. 148. 1796.

Amsonia latifolia Michx. Fl. Bor. Am. **1**: 121. 1803; Pursh, Fl. Am. Sept. ed. 1, **1**: 184. 1814; Roem. & Schult. Syst. Veg. **4**:

432. 1819; Elliott, Sketch Bot. S. C. & Ga. 316. 1821; Darby, Bot. South. States, 434. 1860.

Amsonia tristis Sm. in Rees, Cycl. **35**: end of art. "Tabernaemontana." 1819; A. DC. in DC. Prodr. **8**: 384. 1844.

Ansonia latifolia (Michx.) Raf. New Fl. N. Am. **4**: 58. 1838.

Amsonia Amsonia (L.) Britton, Mem. Torr. Bot. Club **5**: 262. 1894; Britton & Brown, Ill. Fl. **3**: 1. 1898; S. Coulter, Rept. Dept. Geol. Ind. **24**: 880. 1899; Hitchcock, Fl. Kans. 13. 1899; Gattinger, Fl. Tenn. 137. 1901; Mohr, Contr. U. S. Nat. Herb. **6**: 674. 1901; Small, Fl. Southeast. U. S. 935. 1903; Lowe, Miss. State Geol. Surv. Bull. 17: 227. 1921.

Herbaceous perennial from a thickened, slightly woody root; stems 3–10 dm. tall, usually clustered from the base, erect or slightly ascending, branched above, the branches ascending or spreading, occasionally somewhat pubescent when young; leaves alternate, relatively distant, ovate to oblong-elliptic, the bases of the lower obtuse to broadly acute, occasionally sparsely pubescent upon the lower surface when very young; inflorescence relatively small and dense, barely held above the foliage, pedicels 3–5 mm. long; calyx 1–1.5 mm. long, glabrous, the lobes triangular-ovate; corolla salverform, the tube 6–8 mm. long, pubescent without, the lobes 4–6 mm. long, oblong to oblong-lanceolate, spreading; stigmatic-cap about as tall as broad, stigma depressed-capitate; follicles continuous, 8–10 cm. long, rather abruptly acuminate, sessile, glabrous, 5–15-seeded; seeds 5–11 mm. long, oblong in outline, truncate at either end, variously pitted and wrinkled, dark brown.

Distribution: moist woods and waste-lands, river-banks, etc.; South Carolina, Tennessee, Illinois, eastern Missouri, eastern Oklahoma, eastern Kansas, southeastern Arkansas, escaped from cultivation in Massachusetts, New Jersey, Pennsylvania, and Delaware.

Specimens examined:

MASSACHUSETTS: Boston, Back Bay waste-lands, Aug. 12, 1903, *Williams* (G); Hampden, June, 1911, *Knowlton* (NE).

NEW JERSEY: South New England Road, introduced in field, Cold Spring, Cape May Co., July 7, 1918, *Brown* (PBC).

Delaware: Wilmington, waste places, June 3–July 18, 1896, *Commons* (PBC).

Pennsylvania: Oakdale, near Philadelphia, June, 1863, *Martindale* (PBC); Philadelphia, Broad Street & Germantown R. R., 1865, *Martindale 4864* (MBG); Gradyville, Delaware Co., June 9, 1898, *Painter* (PBC); near Philadelphia, May, 1889, *Leeds* (PBC); Gradyville, June 3, 1904, *Vail 546* (US).

South Carolina: Greenville Co., ravines near Caesar's Head, Aug. 5, 1881, *J. D. Smith* (G).

Tennessee: Knoxville, thicket on Tennessee River bank, April and July, 1890, *Ruth 174* (G); Knoxville, April, 1894, *Ruth 466* (P, US); Knoxville, June, 1898, *Ruth 480* (MBG).

Illinois: Chandlersville, Aug. 19, 1886, *Seymour 1584* (G, P).

Missouri: St. Louis, July 2, 1895, *Glatfelter* (G, MBG); St. Louis, date lacking, *Engelmann* (G, MBG); Eagle Rock, uncommon in barrens, June 22, *Bush 11* (MBG, US); uncommon in rich woods, 4 miles e. of Carthage, May 27, 1906, *E. J. Palmer 921* (MBG); Newton Co., cherty barrens, July 15, 1906, *E. J. Palmer 12* (MBG); Carthage, rich woods, May 27, 1906, *E. J. Palmer 818* (MBG); Noel, low ground, May 10, 1915, *Bush 7513* (MBG); Noel, McDonald Co., thickets, hillsides, Sept. 12, 1913, *E. J. Palmer 4305* (MBG); Swan, common in woods, Oct. 4, 1899, *Bush 753* (MBG).

Arkansas: Fort Huron, date lacking, *Edward* (G); Fayetteville, May, year lacking, *Harvey 38* (ANSP); Fulton, low ground, April 17, 1905, *Bush 2378* (MBG); Fayetteville, May 10, 1919, *Wells* (US).

Louisiana: Hammond, April 10, 1889, *Gallup 4* (US).

Oklahoma: Leflore Co., Page, on bank of mountain creek near Rich Mountain, Sept. 8, 1913, *Stevens 2670* (G, US); Page, Leflore Co., on rocky mountain-side, April 25, 1915, *Blakely 3425* (G); Poteau, Leflore Co., July 13, 1915, *E. J. Palmer 8286* (MBG).

Kansas: Cherokee Co., rocky woods, May 7, 1897, *Hitchcock 76a* (MBG).

4a. Var. **salicifolia** (Pursh) Woodson, n. comb.

Amsonia salicifolia Pursh, Fl. Am. Sept. ed. 1, **1**: 184. 1814;

Roem. & Schult. Syst. Veg. **4**: 432. 1819; Elliott, Sketch Bot. S. C. & Ga. 316. 1821; A. DC. in DC. Prodr. **8**: 384. 1844; Darby, Bot. South. States, 434. 1860; Wood, Classbook Bot. 589. 1860; Small, Fl. Southeast. U. S. 935. 1903; Britton, Man. Fl. 737. 1907.

Ansonia salicifolia (Pursh) Raf. New Fl. N. Am. **4**: 58. 1838.

Herbaceous perennial from a slightly thickened root; stems 3–5 dm. tall, usually clustered from the base, erect or slightly ascending, glabrous or very slightly pubescent when young, branched above, the branches ascending or somewhat spreading; leaves alternate, the blades relatively narrow, lanceolate to linear-lanceolate, the lower 5–10 times as long as broad, both the base and the apex narrowly acute to acuminate, glabrous above, glaucous or glaucescent beneath, becoming green in age; inflorescence loose, relatively few-flowered, pedicels 3–7 mm. long; calyx about 1 mm. long, the lobes minutely triangular, glabrous; corolla salverform, the tube relatively narrow, 6–10 mm. long, scatteringly pubescent without, the lobes 5–7 mm. long, lanceolate, spreading; stigmatic-cap somewhat broader than tall, stigma depressed-capitate or truncate; follicles relatively slender, continuous or very slightly torose, 8–10-seeded; seeds 5–10 mm. long, oblong in outline, truncate at either end, variously pitted or wrinkled, brown.

Distribution: river-banks and moist thickets generally; Virginia, North Carolina, South Carolina, Georgia, Alabama, Louisiana, Kentucky, Tennessee, Indiana, Illinois, Missouri, Arkansas, and Texas.

Specimens examined:

Virginia: Petersburg, date lacking, *Tuomey* (ANSP).

North Carolina: Biltmore, river-banks, May 11, 1897, *Biltmore 81b* (G, MBG, US, NY); same locality, May 2, 1896, *Biltmore 81* (MBG); Weldon, April, 1897, *Williamson* (ANSP); same locality, April 19, 1908, *Williamson* (ANSP); Hot Springs, May 5, 1884, *Smith* (ANSP); Warm Springs, May 6, 1887, *Smith* (ANSP); Columbus, 1897, *Townsend* (US); Statesville, May, 1878, *Hyams* (US); Granville Co., May, 1873, *Faxon* (G); Mt. Tryon, Polk Co., moist rich soil on a level spot along a mountain rill, May, 1918, *Millspaugh 4030* (F); Weldon, April 19, 1908, *Bartram* (G); data lacking, *Curtis* (G).

South Carolina: Oconee Co., Clemson College, low woods, April 16, 1906, *House 1851* (US, NY).

Georgia: Thompson's Mills and vicinity, Gwinnett Co., April 8, 1908, *Allard 197* (US); Macon, date lacking, *Green* (ANSP); Stone Mountain, Yellow River, May 3, 1899, *Sargent 69* (G).

Alabama: Albertsville, April 22, 1899, *Hosdy* (US); Chickasaw, rich places in the barrens, April, 1919, *Graves 566* (US); Tuskaloosa, April, 1892, *Ward* (US); Auburn, Lee Co., April 22, 1900, *Earle* (G).

Mississippi: Pass Christian, May 16, 1924, *Cooper* (MBG); Rolling Fork, April, 1895, *Boyce* (US).

Louisiana: Feliciana [East or West?] Parish, *Carpenter* (G); east of Baton Rouge, April 20, 1874, *Joor* (F).

Indiana: banks of the Wabash River, June, 1868, *Allen* (F).

Kentucky: Bowling Green, 1903, *Price* (MBG); barrens of Kentucky River near Hopkinsville, date lacking, *Buckley* (MBG).

Tennessee: Franklin Co., May 5, 1898, *Eggert* (MBG); Nashville, 1880, *Hubbard 2268* (G).

Illinois: exact locality lacking, 1845, *Mead* (G); Grantsburg, April 28, 1900, collector lacking (P); Conologue, April, 1924, *Woodson* (MBG).

Missouri: bank of Meramec River near Windsor Springs, April 19, 1891, *Douglass* (US); Cave Spring, 1887, *Blankinship* (US); Cave Spring, Greene Co., June 18, 1905, *Standley* (US); Tyson, St. Louis Co., May 19, 1918, *Drushel 3757* (MBG); banks of the Meramec River, Minke, St. Louis Co., May 17, 1919, *Greenman 3944* (MBG); Chadwick, May 15, 1907, *Bush 4461* (MBG).

Arkansas: Baker Springs, Howard Co., April 10, 1909, *Kellogg* (MBG); data lacking, *Pitcher* (ANSP).

Texas: Beaumont, low wet woods, March 16, 1918, *E. J. Palmer 13090* (MBG).

4b. Var. Gattingeri Woodson, n. var.[1]

Herbaceous perennial from a thickened slightly woody root;

[1] Var. Gattingeri var. nov., plus-minusve pilosa varietatem genuinam simulans differt foliis longioribus basi acutis; corollae tubo lanoso.—Tennessee, Nashville, June, year lacking, *A. Gattinger* (Gray Herb. TYPE).

stems 3–10 dm. tall, pubescent, becoming glabrous, somewhat clustered at the base, erect or ascending, branched above, the branches ascending or spreading; leaves relatively distant, alternate, the blades lanceolate to linear-lanceolate above, the lower 5–10 times as long as broad, both base and apex narrowly acute to acuminate, green, pubescent, frequently densely so, becoming glabrous in age; inflorescence compact, many-flowered, pedicels 2–4 mm. long; calyx 2–4 mm. long, the lobes narrowly triangular, glabrous, or with a few scattered hairs; corolla salverform, the tube 7–10 mm. long, densely pubescent or villous without, especially in the sinuses of the lobes, the lobes 5–8 mm. long, lanceolate, spreading; stigmatic-cap much broader than tall, stigma truncate; follicles slender, continuous or very slightly torose, 9–14 cm. long, acuminate, sessile, glabrous, 7–11-seeded; seeds 5–12 mm. long, oblong in outline, truncate or slightly tapered at the ends, variously pitted or wrinkled, brown.

Distribution: woods and ravines, northern Georgia, Tennessee, Illinois, Missouri, southeastern Kansas, eastern Oklahoma, and northeastern Texas.

Specimens examined:

Georgia: Jasper City, 1847, *Porter* (G).

Tennessee: Nashville, June, year lacking, *Gattinger* (G type, MBG); Nashville, islands in Cumberland River, September, 1878, *Gattinger* (MBG, NY, ANSP, F).

Kentucky: barrens of the Kentucky River, exact locality lacking, 1860, *Short* (MBG).

Illinois: Athens, 1861, *Hall* (G, P, MBG); Olney, Richmond Co., Turkey Creek bottoms, May 19, 1914, *Ridgway 104* (G, MBG); Grantsburg, April 28, 1900, *Baker* (P); East Hannibal, June 6, 1913, *Davis 398* (MBG, US); along road west of Fish Lake, St. Clair Co., July 16, 1898, *Norton* (MBG); damp shady thickets, American Bottoms, opposite St. Louis, May, 1845, *Engelmann* (MBG); Queens Lake, Clinton Co., May 20, 1917, *Ledman* (MBG); Venedy, May 18, 1926, *Anderson & Woodson 5* (MBG); Conologue, May 16, 1926, *Woodson & Stevenson 41* (MBG).

Missouri: Alba, rich bluff woods, April 29, 1909, *E. J. Palmer 1819* (G, MBG); St. Louis, July 28, 1910, *Sherff 801* (G, F,

MBG); Webb City, gravelly branches, Sept. 2, 1909, *E. J. Palmer 2620* (G, MBG); Winfield, Lincoln Co., June 7, 1916, *Davis 1403* (MBG); Bower's Mill, Lawrence Co., rich hill-side woods, April 22, 1908, *E. J. Palmer* (MBG); Allenton, June 10, 1884, *Kellogg* (MBG); Elmont, May 23, 1914, *Emig* (MBG); Gascondy, July 21, 1914, *Emig 221* (MBG); Gray's Summit, May 15, 1926, *Greenman 4493* (MBG); Allenton, June, 1880, *Letterman* (MBG, US).

Arkansas: Benton Co., date lacking, *Plank* (MBG); Eureka Springs, April 27, 1899, *Trelease* (MBG); Little Rock, May, 1886, *Hasse* (F).

Oklahoma: Miami, on dry bank of draw, Aug. 26, 1913, *Stevens 2337* (G, MBG, US); Page, on rocky mountain-side, April 25, 1915, *Buckley 3425* (G, MBG); rocky hills, Wichita Mts. not common, July, 1891, *Sheldon 224* (MBG).

5. **Amsonia ludoviciana** Vail in Small, Fl. Southeast. U. S. ed. 2, 935. 1913.

Herbaceous perennial from a slightly thickened woody root; stems 5–11 dm. tall, pubescent, at least when young, sparingly branched, erect or ascending, the branches erect or ascending; leaves relatively distant, alternate, the blades elliptic, both base and apex acute to acuminate, 5–8 cm. long, essentially glabrous above, densely white-lanose beneath, pedicels 2–4 mm. long; inflorescence relatively dense, several-flowered, pedicels 2–4 mm. long; calyx 2–3 mm. long, the lobes triangular, 1–1.5 mm. long, pubescent; corolla salverform, the tube 5–9 mm. long, densely pubescent or villous without, the lobes about equalling, or slightly exceeding, the tube, lanceolate, spreading; stigmatic-cap about as broad as tall, stigma truncate; follicles slender, continuous, 8–10 cm. long, acuminate, sessile, manifestly pubescent, 6–10-seeded; seeds 5–12 mm. long, oblong-ovoid in outline, truncate at the ends, variously pitted and wrinkled, dark brown.

Distribution: known only from southern Louisiana.

Specimens examined:

Louisiana: New Orleans, date lacking, *Ingalls* (NY); Shackynody, April, year lacking, *Hale* (NY).

Subgenus II. SPHINCTOSIPHON (K. Schumann) Woodson, n. comb. §*Sphinctosiphon* K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. 4²: 143. 1895; Dalla Torre & Harms, Gen. Siph. 406. 1904.

Bracteoles conspicuous, giving the inflorescence a chaffy appearance; mouth of the corolla-tube markedly constricted at anthesis; stigma apiculate by two distinct obtuse lobes; follicles continuous, not articulated, fibrous, not horny in texture; seeds oblong in outline, truncate at either end, variously pitted and wrinkled; plants of the southwestern United States and northern Mexico. Spp. 6–13.

Section I. MICRANTHAE Woodson. Corolla-tube 1–1.5 cm. long; calyx 1–4 mm. long; follicles 4–7 cm. long; seeds 4–8 mm. long.

KEY TO THE SPECIES

a. Follicles slender; seeds fertile.
  b. Corolla-lobes 3–6 mm. long, ovate or oblong.
    c. Corolla-lobes 3–4 mm. long; plant entirely glabrous.....*6. A. Palmeri*
    cc. Corolla-lobes 5–6 mm. long; plant pubescent, at least the calyx-lobes.
      d. Stem and leaves glabrous; pedicels 3–5 mm. long; inflorescence loose..............................*7. A. pogonosepala*
      dd. Stem and leaves pubescent; pedicels 1–2 mm. long, or practically sessile; inflorescence dense.
        e. Calyx glabrous; inflorescence many-flowered...*8. A. hirtella*
        ee. Calyx pubescent; inflorescence few-flowered...*9. A. Standleyi*
  bb. Corolla-lobes 6–8 mm. long, lanceolate...................*10. A. latifolia*
aa. Follicles short; seeds sterile.............................*11. A. Kearneyana*

6. Amsonia Palmeri Gray, Proc. Am. Acad. **12:** 64. 1877; Gray, Syn. Fl. N. Am. 2¹: 82. 1878. Pl. 52, figs. 14–15.

Amsonia Fremontii Rydb. Bull. Torr. Bot. Club **40:** 465. 1913. *nomen.*

Herbaceous perennial from a somewhat thickened root, glabrous; stems 3–5 dm. tall, usually clustered from the base, erect or slightly ascending, sparingly branched above, the branches ascending; leaves alternate, relatively numerous, oblong-lanceolate to linear-lanceolate above, the blades 2.5–7 cm. long, 4–8 mm. broad; inflorescence relatively few-flowered and loose, held well above the foliage; pedicels 1–3 mm. long, or practically

lacking; calyx 3–4 mm. long, sparsely hairy, the lobes subulate; corolla salverform, the tube constricted at the mouth, 1–1.8 cm. long, the lobes ovate to ovate-oblong, 3–4 mm. long, erect or spreading; stigma apiculate by two distinct obtuse lobes; follicles 4–6 cm. long, acuminate, sessile, glabrous, continuous, 5–10-seeded; seeds 4–8 mm. long, oblong in outline, truncate at either end, variously pitted or wrinkled, chocolate-brown.

Distribution: Arizona and New Mexico.

Specimens examined:

New Mexico: exact locality lacking, 1851–52, *Wright 1669* (G type, MBG).

Arizona: exact locality lacking, 1884, *Lemmon 3248* (G); 50 miles s. of Lee's Ferry, June 12, 1890, *M. E. Jones* (P, US); Hillside, May 1, 1903, alt. 3700 ft., *Jones* (MBG); Beale's Spring, date lacking, *Lemmon & Lemmon* (US); exact locality lacking, 1887, *Mearns 152* (NY).

7. **Amsonia pogonosepala** Woodson, n. sp.[1]

Herbaceous perennial from a thickened woody root; stems 5–8 dm. tall, glabrous, clustered from the base, erect or slightly ascending, freely branched above, the branches ascending or spreading; leaves alternate, relatively numerous, glabrous, lanceolate to oblong-lanceolate, the blades 1–1.5 cm. broad, 5–7 cm. long, acute to acuminate at both base and apex, petiolate, the petioles 1–3 mm. long; inflorescence loose, relatively many-flowered; pedicels 2–4 mm. long; calyx 3–6 mm. long, the lobes subulate, conspicuously ciliate, 2–5 mm. long; corolla salverform, the tube constricted at the orifice, 12–15 mm. long, glabrous without, the lobes 5–6 mm. long, ovate to oblong, spreading; stigma apiculate by two distinct obtuse lobes; follicles 1.2–8 cm. long, acuminate, sessile, glabrous, continuous, 4–15-seeded; seeds 7–10 mm. long, oblong-truncate in outline, variously pitted or wrinkled, reddish brown.

[1] **Amsonia pogonosepala** sp. nov., humila saepe basaliter ramosa 5–8 dm. alta; ramis erectis vel laxe ascendentibus glabris; foliis lanceolatis oblongo-lanceolatis petiolatis 5–7 cm. longis 1–1.5 cm. latis glabris; lobis calycis piloso-ciliatis subulatis 2–5 mm. longis; corollae lobis ovatis vel ovato-oblongis 5–6 mm. longis tubo subclavato dimidio brevioribus distendatis; stigmate subtrochleari apice bilobato; folliculis teretibus gracilibus continuis glabris sessilibus 2–8 cm. longis.—Arizona, dry rocky hills, San Francisco Mts., April, 1881, *H. H. Rusby 256* (MBG type).

Distribution: southern Arizona.

Specimens examined:

ARIZONA: dry rocky hills, San Francisco Mts., April, 1881, *Rusby 256* (MBG TYPE, ANSP, NY); small sandy wash between Apache Junction and Canyon Lake, June 21, 1928, *Harrison & Peebles 5540* (MBG, US); near Mormon Flats, April 1, 1928, *Peebles, Harrison, & Kearney 3820* (US).

8. **Amsonia hirtella** Standley, Proc. Biol. Soc. Wash. **26:** 118. 1913; Wooton & Standley, Contr. U. S. Nat. Herb. **19:** 505. 1915.

Herbaceous perennial from a somewhat thickened root, hirtellous; stems 3–5 dm. tall, usually clustered from the base, erect or somewhat ascending, very sparingly branched above, the branches ascending; leaves alternate to subverticillate above, relatively numerous, lanceolate to linear-lanceolate, the blades 3–5 cm. long, 2–5 mm. broad, sessile to subsessile; inflorescence dense, relatively many-flowered; pedicels 1–2 mm. long or practically lacking; calyx 4–5 mm. long, glabrous, except for a few scattered hairs at the tips, the lobes subulate; corolla salverform, the tube constricted at the mouth, 12–15 mm. long, glabrous without, the lobes 5–6 mm. long, ovate to ovate-oblong, slightly spreading; stigma apiculate by two distinct obtuse lobes; follicles unknown.

Distribution: known only from southwestern New Mexico.

Specimens examined:

NEW MEXICO: Grant Co., cañons, May 1, 1892, *Mearns 117* (US TYPE).

9. **Amsonia Standleyi** Woodson, n. sp.[1] Pl. 52, figs. 16–17.

Herbaceous perennial from a somewhat thickened woody root, densely pubescent; stems 3–5 dm. tall, usually clustered from the base, erect or slightly ascending, freely branched above, the

[1] Amsonia Standleyi sp. nov., pilosa humila saepe basaliter ramosa 3–5 dm. alta; ramis erectis vel laxe ascendentibus; foliis lanceolatis linearibusque plerumque sessilibus 3–7 cm. longis 4–10 mm. latis alternis vel subverticillatis; lobis calycis pilosis lineari-lanceolatis 4–5 mm. longis; corollae lobis ovatis vel ovato-oblongis 5–6 mm. longis tubo subclavato dimidio brevioribus distendatis; stigmate subtrochleari apice bilobato; folliculis teretibus gracilibus continuis glabris sessilibus 6–7 cm. longis.—New Mexico, 1851–52, *C. Wright* (Gray Herb. TYPE).

branches ascending or slightly spreading; leaves alternate to subverticillate above, relatively numerous, lanceolate to linear-lanceolate, the blades 3–7 cm. long, 4–10 mm. broad, narrowed to an inconspicuous petiole, or practically sessile; inflorescence dense, relatively few-flowered; pedicels 1–2 mm. long, or practically lacking; calyx 4–5 mm. long, densely pubescent throughout, the lobes subulate; corolla salverform, the tube constricted at the mouth, 8–10 mm. long, glabrous without, the lobes ovate to ovate-oblong, 5–6 mm. long, spreading; stigma apiculate by two distinct obtuse lobes; follicles 6–7 cm. long, acuminate, sessile, glabrous, continuous, 5–10-seeded; seeds 4–8 mm. long, oblong in outline, truncate at either end, variously pitted and wrinkled, brown.

Distribution: Texas, New Mexico, and Chihuahua.

Specimens examined:

UNITED STATES:

TEXAS: Bofecillos, May 18, 1881, *Havard* (US).

NEW MEXICO: exact locality lacking, 1851–52, *Wright* (G TYPE).

MEXICO:

CHIHUAHUA: Candelaria, Oct. 24, 1911, *Stearns 228* (US).

This species is named in honor of Mr. Paul C. Standley, who provisionally referred the Havard and Stearns specimens, bearing fruit only, to *A. hirtella*, in describing that species, but foresaw that when the flowers corresponding to the fruit should be found they would constitute a new species.

10. Amsonia Jonesii Woodson, new name.

Amsonia latifolia M. E. Jones, Contr. West. Bot. **12:** 50. 1908, not Michx.; Rydb. Fl. Rocky Mts. 668. 1917; Tidestrom, Contr. U. S. Nat. Herb. **25:** 418. 1925.

Amsonia texana Rydb. Fl. Rocky Mts. 668. 1917, not Heller.

Herbaceous perennial from a thickened, frequently very woody root, glabrous; stems 2–4 dm. tall, usually much clustered from the base, erect or ascending, sparingly branched, the branches ascending; leaves alternate, numerous, ovate to ovate-oblong, glaucous, the blades 3–5 cm. long, 1–2 cm. broad, petiolate; inflorescence dense, relatively many-flowered; pedicels 3–5 mm.

long; calyx about 1.5 mm. long, the lobes triangular; corolla salverform, 5–8 mm. long, the lobes narrowly oblong-lanceolate, 5–7 mm. long, spreading, slightly pubescent at the tips when in aestivation; stigma apiculate by two distinct obtuse lobes; follicles 5–8 cm. long, acuminate, sessile, glabrous, continuous, 4–8-seeded; seeds 4–6 mm. long, oblong in outline, transversely truncate at either end, variously pitted and sculptured, brown.

Distribution: rocky gorges and canons, southwestern Colorado, southeastern Utah, and northeastern Arizona.

Specimens examined:

COLORADO: Grand Junction, alt. 4500 ft., June 21, 1894, *M. E. Jones 5469* (P); Grand Junction, alt. 4000 ft., May 28, 1895, *M. E. Jones* (P); McElmo Creek, Montezuma Co., July 19, 1895, *Eastwood 72* (G, MBG); Grand Junction, June 21, 1894, *Jones 5476q* (MBG, ANSP, US, NY).

UTAH: Monroe, Sevier Co., alt. 5000 ft., May 24, 1894, *M. E. Jones 6446* (P TYPE, MBG).

ARIZONA: Navajo Wells, alt. 5000 ft., May 24, 1894, *M. E. Jones 5289aa* (P, MBG); Pagumpa, alt. 4000 ft., April 21, 1894, *M. E. Jones 5093* (P, US, NY, MBG).

11. Amsonia Kearneyana Woodson, n. sp.[1]

Herbaceous perennial from a thickened, somewhat woody root, more or less pilose; stems 4–8 dm. tall, usually clustered from the base, erect or ascending, sparingly branched, the branches ascending; leaves alternate to subverticillate, oblong-lanceolate to lanceolate, 4–7 cm. long, 1–1.5 cm. broad, petiolate, or subsessile; inflorescence dense, many-flowered; pedicels 1 mm. long or practically lacking; calyx 3–5 mm. long, the lobes subulate-aristate, densely pilose-ciliate; corolla salverform, the tube constricted at the orifice, 1–1.2 cm. long, the lobes 3–5 mm. long, oblong to ovate, erect or slightly spreading; stigma apiculate by two distinct obtuse lobes; follicles short and obviously de-

[1] Amsonia Kearneyana sp. nov., plus-minusve pilosa basaliter ramosa 4–8 dm. alta; ramis ascendentibus; foliis alternis vel subverticillatis subsessilibus oblongo-lanceolatis 4–7 cm. longis 1–1.5 cm. latis; lobis calycis subulato-aristatis 3–5 mm. longis; corollae tubo longo subclavato 1–1.2 cm. longo lobis ovatis 3–5 mm. longis erectis vel ascendentibus; stigmate subtrochleari apici bilobato; folliculis deformis; seminibus sterilibus.—Arizona, Pima Co., South Cañon, April 9, 1928, *F. Thackery 55* (MBG TYPE).

formed but essentially continuous, 2–5 cm. long, 5–7 mm. broad; seeds sterile.

Distribution: southern Arizona.

Specimens examined:

Arizona: South Canyon, Baboquivari Mts., May 24, 1926, *Thackery 2018* (US, MBG); South Canyon, Baboquivari Mts., March 29, 1927, *Peebles, Harrison & Kearney 3820* (US, MBG); South Cañon, Pima Co., April 9, 1928, *Thackery 55* (MBG type).

Because of its appearance intermediate between *A. Standleyi* or *A. Palmeri* and *A. brevifolia* or *A. tomentosa*, because of its geographical position, and because of its complete sterility, *A. Kearneyana* is regarded as a natural hybrid between the subgenera *Sphinctosiphon* and *Articularia*. The flowers are decidedly of the type of *A. Palmeri*, with oblong-ovate, erect or ascending corolla-lobes, while the broad foliage is very similar to that of *A. brevifolia* or *A. tomentosa*. However, since several colonies have been found in the same general vicinity, it is thought better to consider it as a distinct species in the light of recent opinions concerning the origin of species by means of hybridization. Since it demonstrates its recent creation by its sterility and its irregular pilosity, it should probably be considered the most recently evolved species of the genus *Amsonia*.

A. Kearneyana is so named in honor of Mr. T. H. Kearney, of the United States Bureau of Plant Industry, who brought the plant to the attention of the author, and furnished much valuable information regarding the genus in Arizona.

Section ii. Longiflorae Woodson. Corolla-tube 3–4 cm. long; calyx 4–8 mm. long; follicles 7–9 cm. long; seeds 5–12 mm. long.

Key to the Species

a. Plant glabrous; corolla-lobes 11–13 mm. long .... 12. *A. longiflora*
aa. Plant pubescent; corolla-lobes 5–7 mm. long .... 13. *A. salpignantha*

12. Amsonia longiflora Torr. Bot. Mex. Bound. Surv. 159. 1859; Gray, Syn. Fl. N. Am. 2[1]: 82. 1878; Hemsley, Biol. Cent.-Am. Bot. 2: 308. 1881; Wooton & Standley, Contr. U. S. Nat. Herb. 19: 504. 1915. Pl. 52, figs. 18–20.

Herbaceous perennial from a thickened somewhat woody root,

glabrous; stems 3.5–6 dm. tall, usually clustered from the base, erect or ascending, copiously branched at maturity, the branches ascending or spreading; leaves alternate to subverticillate, linear-lanceolate to filiform, 2.5 cm. long, 1–2 mm. broad, sessile; inflorescence relatively loose, usually containing only 5–10 flowers; pedicels 2–5 mm. long; calyx 6–8 mm. long, the lobes subulate-aristate; corolla trumpet-shaped, the tube constricted at the mouth, 3–4 cm. long, the lobes 11–13 mm. long, oblong-lanceolate, spreading; stigma apiculate by two distinct obtuse lobes; follicles slender, continuous, 7–9 cm. long, acuminate, sessile, 5–15-seeded; seeds 5–10 mm. long, elliptic-oblong in outline, truncate at either end, variously pitted or wrinkled, brown.

Distribution: southeastern New Mexico, extreme western Texas, and north-central Mexico.

Specimens examined:

UNITED STATES:

TEXAS: El Paso, 1881, *Vasey* (G, US, MBG); Hood Co., dry rocky prairie, Sept. 5, 1903, *Reverchon 3881* (MBG); El Paso, April, 1852, *Parry* (MBG); El Paso, rocky ravines, *Wright 1168* (G, NY TYPE, MBG); data lacking, *Wright 72* (NY).

NEW MEXICO: base of Sacomento Mt., Alamogordo, April 14, 1902, *Rehn & Viereck* (ANSP); in arroyo, base of foothills, Alamogordo, May 19, 1902, *Rehn & Viereck* (ANSP); Rio Gila, Aug. 15, 1902, *Wooton* (US).

ARIZONA: Sonoika Creek, south of Patagonia, April 15, 1908, *Tidestrom 848* (US).

MEXICO:

DURANGO: vicinity of the city of Durango, April–Nov., 1896, *E. Palmer 90* (G, MBG, NY).

13. **Amsonia salpignantha** Woodson, n. sp.[1] Pl. 52, figs. 21–22.

Herbaceous perennial from a thickened somewhat woody root,

[1] **Amsonia salpignantha** sp. nov., pilosa vel scabra basaliter ramosa 2–3.5 dm. alta; ramis erectis vel ascendentibus; foliis multis alternis vel subverticillatis sessilibus lineari-lanceolatis filiformibusque 2–5 cm. longis .5–4 mm. latis; lobis calycis lineari-lanceolatis 4–5 mm. longis; corollae tubo longo subclavato 3–4 cm. longo; corollae lobis ovatis 5–7 mm. longis distendatis; stigmate subtrochleari apici bilobato; folliculis teretibus gracilibus continuis glabris sessilibus 7–9 cm. longis.—Texas, Hamilton Co., rocky prairies on the Cowhouse Creek, May, 1884, *J. Reverchon 1557* (MBG TYPE).

pubescent, scabrous in age; stems 2–3.5 dm. tall, usually clustered from the base, erect or ascending, branched, the branches ascending; leaves numerous, alternate to subverticillate, linear-lanceolate to filiform, 2–5 cm. long, .5–4 mm. broad, sessile; inflorescence relatively dense, containing usually 10–30 flowers; pedicels 1–4 mm. long, or practically lacking; calyx 4–5 mm. long, the lobes subulate or narrowly lanceolate; corolla trumpet-shaped, the tube constricted at the mouth, 3–4 cm. long, glabrous without, the lobes 5–7 mm. long, oblong-ovate, spreading; stigma apiculate by two distinct obtuse lobes; follicles slender, continuous, 7–9 cm. long, acuminate, sessile, 5–15-seeded; seeds 5–12 mm. long, oblong in outline, truncate at either end, variously pitted or wrinkled, brown.

Distribution: southwestern Texas and Chihuahua.

Specimens examined:

United States:

Texas: Hamilton Co., 1885, *Reverchon 99* (G, MBG); exact locality and date lacking, *Pope* (G); rocky prairies on the Cowhouse Creek, Hamilton Co., May, 1884, *Reverchon 1557* (F, MBG type); Limpio Mts., 1883, *Havard* (US); Austin, 1880, *Oberwetter* (US); Del Rio, Dec. 7, 1891, *Plank* (NY).

Mexico:

Chihuahua: exact locality lacking, 1852, *Wright 1671* (G).

Subgenus III. Articularia Woodson

Subgenus III. Articularia Woodson, n. subgen.

§*Sphinctosiphon* K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. 4^2: 143. 1895, in part; Dalla Torre & Harms, Gen. Siph. 406. 1904, in part.

Bracteoles conspicuous, giving the inflorescence a somewhat chaffy appearance; mouth of the corolla-tube markedly contracted in anthesis; stigma apiculate by two distinct obtuse lobes; follicles torose, articulated into thickish constricted segments, horny, not fibrous in texture; seeds elliptic in outline, rounded or pointed at the ends, rarely truncate, relatively smooth and corky; plants of the southwestern United States and northern Mexico. Spp. 14–17.

Key to the Species

a. Plant glabrous, or with but scattered hairs.
  b. Leaves ovate to ovate-lanceolate above; corolla-tube about 10 mm. long .... *14. A. brevifolia*
  bb. Leaves lanceolate to linear above; corolla-tube about 15 mm. long. .... *15. A. Eastwoodiana*
aa. Plant villous or tomentose.
  b. Leaves ovate to ovate-lanceolate, petiolate .... *16. A. tomentosa*
  bb. Leaves lanceolate to linear, sessile or subsessile .... *17. A. arenaria*

14. Amsonia brevifolia Gray, Proc. Am. Acad. **12**: 64. 1877; Gray, Syn. Fl. N. Am. 2^1: 81. 1878; Watson, Bot. Cal. **2**: 462. 1880; Coville, Contr. U. S. Nat. Herb. **4**: 142. 1893; Wooton & Standley, Contr. U. S. Nat. Herb. **19**: 505. 1915; Rydb. Fl. Rocky Mts. 668. 1917; Davidson & Moxley, Fl. South. Cal. 278. 1923; Tidestrom, Contr. U. S. Nat. Herb. **25**: 418. 1925; Jepson, Man. Fl. Pl. Cal. 768. 1925. Pl. 53, figs. 26–28.

Herbaceous perennial from a thickened fibrous root, glabrous; stems 1.5–3.5 dm. tall, usually clustered from the base, erect or ascending, sparingly branched; leaves alternate, numerous, ovate-oblong to oblong-lanceolate, 2–3 cm. long, .5–1.5 cm. broad, acute to acuminate at either end; inflorescence dense, much divided at maturity; pedicels .5–1.5 mm. long or practically lacking; calyx 2–4 mm. long, the lobes subulate, bluish tinted; corolla salverform, the tube constricted at the mouth, 7–10 mm. long, the lobes ovate to ovate-oblong, 4–6 mm. long, spreading; stigma apiculate by two distinct obtuse lobes; follicles 5–7 cm. long, torose, articulated into thickish constricted segments, sessile, glabrous, 3–10-seeded; seeds 5–7 mm. long, elliptic-lanceolate in outline, sharply truncate at one or both ends, never tapering sharply, 8–10 mm. long, 3.5–4 mm. broad, smooth or slightly wrinkled, yellowish-brown.

Distribution: deserts and mountain slopes, southwestern Utah, northwestern Arizona, southern Nevada, and southern California.

Specimens examined:

Utah: Kanab, Logan Co., 1872, *Thompson* (G); exact locality and date lacking, 1874, *Parry* (G); Garfield Co., 1883, *Siler* (ANSP).

Arizona: Mokiah Pass, 1877, *E. Palmer 302* (G type).

Nevada: Eldorado Cañon at Nelson, alt. 3000 ft., April 30, 1907, *M. E. Jones* (P); 22 miles south of Searchlight, March 26, 1924, *Jaeger* (P); Las Vegas, June, 1915, *K. Brandegee* (P); Ashmeadows, alt. 3000–4000 ft., May–Oct. 1898, *Purpus 5988* (P); Cottonwood Springs, Las Vegas Valley, April 30, 1891, *Bailey 1885* (US).

California: Mojave region, June, 1876, *E. Palmer 435* (G, MBG, ANSP, US); Mojave Desert near San Bernardino, 1880, *Lemmon* (G); Colorado Desert, in desert sands, April 24, 1921, *Spencer 1778* (G); San Bernardino, May, 1882, *Parish 1332* (G, MBG, US); San Bernardino Co., north slope of San Bernardino Mts., alt. 4000–6000 ft., June 15, 1895, *Parish 3765* (G); Hesperia, in desert sand, Mojave Desert, alt. 3100 ft., May 8, 1917, *Spencer 347* (G, P); Kelso, alt. 3000 ft., May 2, 1906, *M. E. Jones* (P); Keyes' Ranch, alt. 3500 ft., common along a wash, May 7, 1922, *Munz & Johnston 5253* (Baker); Corn Springs, rocky slope, high gorge, alt. 2500 ft., *Munz & Keck 4843* (Baker); Goffs, Mohave Desert, March 28, 1924, *Jaeger* (P); entrance to Deep Creek, slope of San Bernardino Mts., alt. 3500 ft., May 9, 1921, *Jaeger 288* (Baker); Quail Springs, Morango Pass, alt. 4000 ft., April 30, 1921, *Munz 4535* (Baker); Cactus Flat, San Bernardino Co., alt. 6000 ft., June 25, 1926, *Munz 10505* (Baker); Cotton-wood Springs, E. Riverside Co., March 26, 1926, *Jaeger* (P); Cushenberry Canyon, San Bernardino Co., June 1, 1892, *Parish 2411* (F); Willow Creek Mt., Panamint Mts., May 22, 1891, *Coville & Funston 825* (US); Mojave Desert, April–May, 1906, *Saunders* (ANSP); Cottonwood Pass, Riverside Co., May, 1905, *Hall 6006* (US); same locality, April 12, 1924, *Evermann* (MBG).

As an instance of the manner in which specific criteria have been applied in the present paper, the case of the specific individuality of *A. brevifolia* Gray and *A. tomentosa* Torr. & Frém. may be of interest, particularly to southwestern botanists. The two species mentioned are both members of the subgenus *Articularia* and inhabit portions of southern California, southern Nevada, and southwestern Utah, and are seldom found separately. Jepson,[1] in 1925, came to the decision that they rep-

[1] Jepson, W. L. Man. Fl. Pl. Cal. 768. 1925.

resented variation only, and reduced *A. tomentosa* to a variety of *A. brevifolia,* although if either should be reduced, the former should remain since it antedates the latter by thirty-two years. The important difference between the two species is the remarkable pubescence of *A. tomentosa,* a character which is not known to vary, judging from the copious herbarium material which the writer has been privileged to examine. *A. tomentosa* is always remarkably pubescent, even to the mature follicles, while *A. brevifolia* is always found to be completely glabrous. Moreover, the seeds of the two species are distinct, a fact which is evidently little appreciated. The seeds of *A. brevifolia* are sharply truncate at one or both ends and never taper sharply, measuring 8–10 mm. long and 3.5–4 mm. broad. The seeds of *A. tomentosa* taper decidedly at both ends and are slightly arcuate, measuring from 12 to 13 mm. long and 3 to 4 mm. broad. Illustrations of the seeds are to be found in pl. 53. In the presence of the seed difference and the non-intergradation of the pubescence or glabrousity of the two species, it has been thought advisable to treat the species as representing a striking affinity rather than as varieties.

15. A. Eastwoodiana Rydb. Bull. Torr. Bot. Club **40:** 465. 1913; Rydb. Fl. Rocky Mts. 668. 1917; Tidestrom, Contr. U. S. Nat. Herb. **25:** 418. 1925.

Herbaceous perennial from a thickened fibrous-woody root, glabrous; stems clustered from the base, 3–5 dm. tall, erect or ascending, branched from near the base, the branches ascending or spreading; leaves alternate, rather distant, oblong-lanceolate below to linear-lanceolate above, 3–5 cm. long, .3–1 cm. broad, acute at either end, subsessile; inflorescence relatively small, loose; pedicels 4–7 mm. long; calyx 2–2.5 mm. long, the lobes subulate; corolla salverform, the tube constricted at the mouth, 1–2 cm. long, the lobes 4–6 mm. long, oblong, spreading; stigma apiculate by two distinct obtuse lobes; follicles 5–8 cm. long, torose, articulated into thickish constricted segments, sessile, glabrous, 3–5-seeded; seeds elliptic in outline, tapered at one or both ends, 14–15 mm. long, 4–5 mm. broad, smooth or slightly wrinkled, reddish brown.

Distribution: stream margins and ravines, Utah and Arizona.

Specimens examined:

Utah: San Juan Co., Willow Creek, July 14, 1895, *Eastwood 73* (G, MBG); San Rafael Swell, Emery Co., May 12, 1914, *M. E. Jones* (P); Moab, June 6, 1913, *M. E. Jones* (P); 10 miles east of Holbrook, June 22, 1901, *Ward* (NY type, US).

Arizona: Lee's Ferry, June 13, 1890, *M. E. Jones* (P, MBG); Kayenta, 1922, *Weatherill* (NY).

16. **Amsonia tomentosa** Torr. & Frém. in Frém. Rept. 1843–44, 316. 1845; Walpers, Ann. Bot. Syst. **1**: 504. 1849; Rept. Torr. Bot. Mex. Bound. Surv. 158. 1859; Gray, Syn. Fl. N. Am. **2**[1]: 81. 1878; Hemsley, Biol. Cent.-Am. Bot. **2**: 308. 1881; Rydb. Fl. Rocky Mts. 668. 1917; Davidson & Moxley, Fl. South. Cal. 278. 1923; Tidestrom, Contr. U. S. Nat. Herb. **25**: 418. 1925. Pl. 53, figs. 23–25.

Amsonia brevifolia Gray var. *tomentosa* (Torr. & Frém.) Jepson, Man. Fl. Pl. Cal. 768. 1925.

Herbaceous perennial from a slightly woody root, densely tomentose; stems 3–4 dm. tall, usually clustered at the base, erect or ascending, branched, the branches ascending or spreading; leaves alternate, rather numerous, ovate-oblong below to oblong-lanceolate above, 2–4 cm. long, 1–1.5 cm. broad, acute at either end, the apices of the upper leaves conspicuously attenuate; inflorescence small, very dense, usually held well above the foliage; pedicels .5–2 mm. long or practically lacking; calyx 2–3 mm. long, the lobes subulate; corolla salverform, the tube 5–8 mm. long, markedly constricted at the mouth, the lobes 4–7 mm. long, ovate to oblong, spreading; stigma apiculate by two distinct obtuse lobes; follicles 6–8 cm. long, articulated into thickish constricted segments, sessile, conspicuously tomentose, 3–7-seeded; seeds elliptic in outline, sharply tapering at both ends, and slightly arcuate, 12–13 mm. long, 3–4 mm. broad, reddish-brown.

Distribution: mountain slopes and deserts, southern Nevada and southern California.

Specimens examined:

Nevada: Eldorado Canon at Nelson, alt. 3000 ft., April 30, 1907, *M. E. Jones* (P).

CALIFORNIA: Cactus Ranch, Cushenberry Canon, San Bernardino Co., alt. 5500 ft., June 1, 1892, *Parish 2412* (G); Mojave Desert, San Bernardino Co., June 5, 1915, *Parish 10244* (G); San Bernardino Co., north slopes San Bernardino Mts., alt. 4000–6000 ft., June 15, 1895, *Parish 3769* (G); Colorado Desert, in desert sands, alt. 3190 ft., 1921, *Spencer 1778a* (G); One-thousand Palms Canon, upper portion Colorado Desert, April 1, 1921, *Jaeger 60* (Baker); Kelso, alt. 4000 ft., May 2, 1906, *M. E. Jones* (P, MBG); One-thousand Palms Canon, alt. 2700 ft., April 10, 1921, *Jaeger 1173* (Baker); Keyes' Ranch, alt. 3500 ft., common along wash, May 7, 1922, *Munz & Johnston 5252* (Baker); vicinity of Corn Springs, Chuckwalla Mts. Colorado Desert, rocky slope in high gorge, alt. 2500 ft., April 9–12, 1922, *Munz & Keck* (Baker).

17. **Amsonia arenaria** Standley, Proc. Biol. Soc. Wash. **26**: 118. 1913; Wooton & Standley, Contr. U. S. Nat. Herb. **19**: 505. 1915. Pl. 53, figs. 29–30.

Herbaceous perennial from a thickened slightly woody root, tomentose; stems 2–4 dm. tall, clustered from the base, erect or ascending, branched, the branches short, ascending; leaves numerous, crowded, alternate to subverticillate, sessile, linear-lanceolate to filiform, slightly fleshy, the midveins usually furrowed, 4–6 cm. long, 1–5 mm. wide; inflorescence dense, not usually held above the foliage; pedicels .5–3 mm. long or practically lacking; calyx 4–7 mm. long, the lobes subulate; corolla salverform, the tube 8–10 mm. long, the lobes ovate-oblong to ovate-lanceolate, 5–8 mm. long, spreading; stigma apiculate by two distinct obtuse lobes; follicles glabrous, 5–8 cm. long, torose, articulated into 2–7 thickish constricted segments, sessile, glabrous, 2–7-seeded; seeds 1–1.5 cm. long, elliptic-arcuate in outline, sharply tapering at both ends, 3–4 mm. broad, nearly smooth, light brown.

Distribution: gravelly plains and mountain slopes; Texas, New Mexico, Arizona, and Chihuahua.

Specimens examined:

UNITED STATES:

TEXAS: exact locality lacking, 1857, *Thurber 138* (F).

New Mexico: San Andreas Mts., 1913, *Wooton* (G, US); exact locality lacking, 1852, *Wright 1670* (G, MBG); Turney Range, Dona Ana Co., Sept. 23, 1912, *Wooton* (US); Strauss, rolling hills, 1912, *Stearns* (MBG).

Arizona: Cameron, infrequent, sand, June 7, 1922, *Hanson 160* (F); same locality, along wash, June 8, 1922, *Hanson 159* (MBG).

Mexico:

Chihuahua: between Laguna de Guzman and Laguna Santa Maria, July 16, 1891, *Hartmann 724* (G); gravelly plains near Lake Guzman, alt. 4000 ft., April 9, 1898, *Pringle 6796* (G, P, MBG); among rocks, Ojo de Vaca to Los Plagas, June, 1851, *Thurber 315* (G).

Species Excluded

Amsonia orientalis Decne. in Jacquemont, Voy. Ind. **4:** 105. 1841 = **Rhazya orientalis** (Decne.) A. DC. in DC. Prodr. **8:** 386. 1844.

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Albrecht, N. — (3).
Allard, H. A. *197* (4a).
Allen, T. F. — (4a).
Anderson, E. S. & Woodson, R. E., Jr. *5* (4b); *4000* (2a).
Arséne, Bro. — (2a).
Bailey, V. *1885* (15).
Baker, C. F. — (4b).
Bartlett, H. H. *1493* (2a).
Bartram, E. B. — (4a).
Berg, N. K. — (2).
Biltmore Herb. *81*, *81b* (4a).
Blakely, G. *3425* (4).
Blankinship, J. W. — (4a).
Boyce, S. S. — (4a).
Brandegee, K. — (14).
Bray, W. L. *60*, *239* (2).
Brown, O. E. — (4).
Buckley, S. B. — (2a); — (4a).
Bush, B. F. *646* (2b); *11*, *753*, *2378*, *7513* (4); *4461* (4a).
Canby, W. M. *68* (2).
Carpenter, — (4a).
Chapman, A. W. — (1); — (2); — (2a).
Clemens, Mrs. J. *11727* (2b).
Commons, A. — (4).
Cooper, C. H. — (4a).
Coville, F. V. & Funston, F. *825* (14).
Curtis, M. A. — (1); — (2); — (2a); — (4a).
Curtiss, A. H. *6820* (1); *2269*, *6376* (2); *6476* (2a).
Davis, J. *398*, *1403* (4b).
Donnell-Smith, J. — (2a); — (4).
Douglass, E. — (4a).
Drushel, J. A. *4572* (2); *3757* (4a).
Durand, A. — (2).
Earle, F. S. — (4a).
Eastwood, A. *72* (10); *73* (15).
Edward, K. — (4).
Eggert, H. — (2); — (2b); — (4a).
Emig, W. H. *399* (2b); — (4b).
Engelmann, G. — (4); — (4b).

Evermann, B. W. — (14).
Faxon, C. E. — (4a).
Fell, M. — (2a).
Gallup, L. *4* (4).
Gattinger, A. — (4b).
Glatfelter, J. M. — (4).
Graves, E. W. *566* (4a).
Green, J. N. — (2a); — (4a).
Greenman, J. M. *3944* (4a); *4493* (4b).
Hale, — (5).
Hall, E. *515* (2b); — (4b).
Hall, H. M. *6006* (14).
Hanson, H. C. 159, 160 (17).
Harper, R. M. *440*, *448*, *606* (1); *1319* (2); *577*, *915*, *1166*, *2138* (2a).
Harrison, G. J. & Peebles, R. H. *5540* (7).
Hartmann, C. V. *724* (17).
Harvey, F. L. *38* (4).
Hasse, —. — (4b).
Havard, V. — (9); — (13).
Hitchcock, A. S. — (2a); *76a* (4).
Hopkins, M. H. *83* (2a).
Hosdy, J. B. — (4a).
Houghton, M. *3606* (2b).
House, H. D. *1851* (4).
Hubbard, G. W. *2268* (4a).
Huger, A. M. — (2a).
Hyams, M. E. — (4a).
Ingalls, T. J. — (5).
Jaeger, E. C. — (14); *288* (14); *60*, *1173* (16).
Jermy, G. *145* (2b).
Jones, M. E. — (6); —, 5289aa, 5469, 5093, 5476q, 6446 (10); — (14); — (15); — (16).
Joor, J. F. — (4a).
Kellogg, J. H. — (4a); — (4b).
Knowlton, C. H. — (4).
Ledman, O. S. — (4b).
Lemmon, J. G. *3248* (6); — (14).
Lemmon, J. G. & Lemmon, — (6).
Letterman, G. W. — (2a); — (4b).
Lindheimer, F. — (2b); *660*, *4* (2b).
Martindale, J. C. —, *4864* (4).
Matsumura, J. — (3).
Maximowicz, K. J. — (3).
Mead, S. B. — (4a).
Mearns, E. A. *152* (6); *117* (8).
Meislahn, M. *210* (2a).
Millspaugh, C. F. *4030* (4a).
Mohr, C. — (2a).
Munz, P. A. *4535*, *10505* (14).
Munz, P. A. & Johnston, I. M. *5253* (14); *5252* (16).
Munz, P. A. & Keck, D. *4843* (14); — (16).
Nash, G. V. *2546* (2a).
Nehrling, H. *12* (2a).
Norton, G. B. S. — (4b).
Oberwetter, P. H. — (13).
Olney, S. T. & Metcalfe, J. *76* (2).
Painter, J. H. — (4).
Palmer, E. *90* (12); *302*, *435* (14).
Palmer, E. J. *27233* (2); *33031* (2a); *11471*, *11616*, *12233*, *12262*, *12597*, *13496*, *24203* (2b); *12*, *818*, *921*, *4305*, *8286* (4); *13090* (4a); —, *1819*, *2620* (4b).
Parish, S. B. *1332*, *2411*, *3765* (14); *2412*, *3769*, *10244* (16).
Parry, C. C. — (12); — (14).
Peebles, R. H., Harrison, G. J. & Kearney, T. H. *3820* (11); *5258* (15).
Pitcher, — (4a).
Plank, E. N. — (2); — (4b); — (13).
Pope, J. — (13).
Porter, T. C. — (2a); — (4b).
Price, S. F. — (4a).
Pringle, C. G. *6796* (17).
Purpus, C. A. *5988* (14).
Ravenel, H. W. — (2).
Rehn, J. A. G. & Viereck, H. L. — (12).
Reverchon, J. *84* (2a); —, *598*, *3122* (2b); *3881* (12); *99*, *1557* (13).
Ridgway, R. *104* (4b).
Rodman, M. — (2).
Rugel, F. — (1); *21* (2a).
Rusby, H. H. *256* (7).
Ruth, A. *241* (2b); *174*, *466*, *480* (4).
Sargent, C. S. — (2); *69* (4a).
Saunders, C. F. — (14).
Seymour, A. B. *1584* (4).
Sheldon, C. S. *224* (4b).
Sherff, E. *801* (4b).
Short, C. W. — (4b).

Siler, A. L. — (14).
Smith, A. H. — (4a).
Spencer, M. F. *1778*, *347* (14); *1778a* (16).
Standley, P. C. — (4a).
Stanfield, S. W. — (2).
Stearns, E. *228* (9); — (17).
Stevens, G. W. *29* (2b); *2670* (4); *2337* (4b).
Sydone, O. — (2b).
Taylor, K. A. — (2).
Thackery, F. H. *2018* (11).
Thompson, Mrs. A. P. — (14).
Thurber, G. *138*, *315* (17).
Tidestrom, I. *848* (12).
Townsend, E. C. — (4a).
Tuomey, M. — (4a).
Vail, W. *546* (4).
van der Velden, A. & W. — (2).
Vasey, G. R. — (12).
Ward, L. F. — (4a); — (15).
Weatherill, J. — (15).
Wells, E. — (4).
Wilkins, T. — (2).
Williams, E. F. — (4).
Williamson, C. S. — (2a); — (4a).
Woodson, R. E., Jr. — (4a).
Woodson, R. E., Jr. & Stevenson, J. *41* (4b).
Wooton, E. O. — (12); — (17).
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Explanation of Plate

PLATE 50

Map of the geographical distribution of *Amsonia* in North America.

oooo subgenus *Euamsonia* (K. Schumann) Woodson.

- *A. Tabernaemontana.*
- *A. ciliata.*
- *A. rigida.*
- ••••• *A. ludoviciana.*

subgenus *Sphinctosiphon* (K. Schumann) Woodson.

- *A. Palmeri.*
- •••• *A. Standleyi.*
- + + + *A. Kearneyana.*
- *A. longiflora.*
- *A. salpignantha.*
- *A. Jonesii.*
- ▲ *A. hirtella.*

subgenus *Articularia* Woodson.

- *A. brevifolia.*
- *A. tomentosa.*
- •••• *A. Eastwoodiana.*
- *A. arenaria.*

NOTE: Since the preparation of Plate 50, *Amsonia ciliata* var. *tenuifolia* has been found locally in extreme south-central Missouri (*E. J. Palmer 33031; Anderson & Woodson 4000*), thus extending the known distribution of that species from central Arkansas.

WOODSON—STUDIES IN APOCYNACEAE

Explanation of Plate

PLATE 51

Illustrations of the subgenus *Euamsonia*, with comparison to *Haplophyton;* all figures × 2 except when otherwise noted.

Haplophyton cimicidium A. DC.

Fig. 1. Flower. × 1.
Fig. 2. Front and side of stamen.
Fig. 3. Pistil.

A. rigida Shuttlew.

Fig. 4. Flower.
Fig. 5. Front and side of stamen.
Fig. 6. Pistil.

A. ciliata Walt.

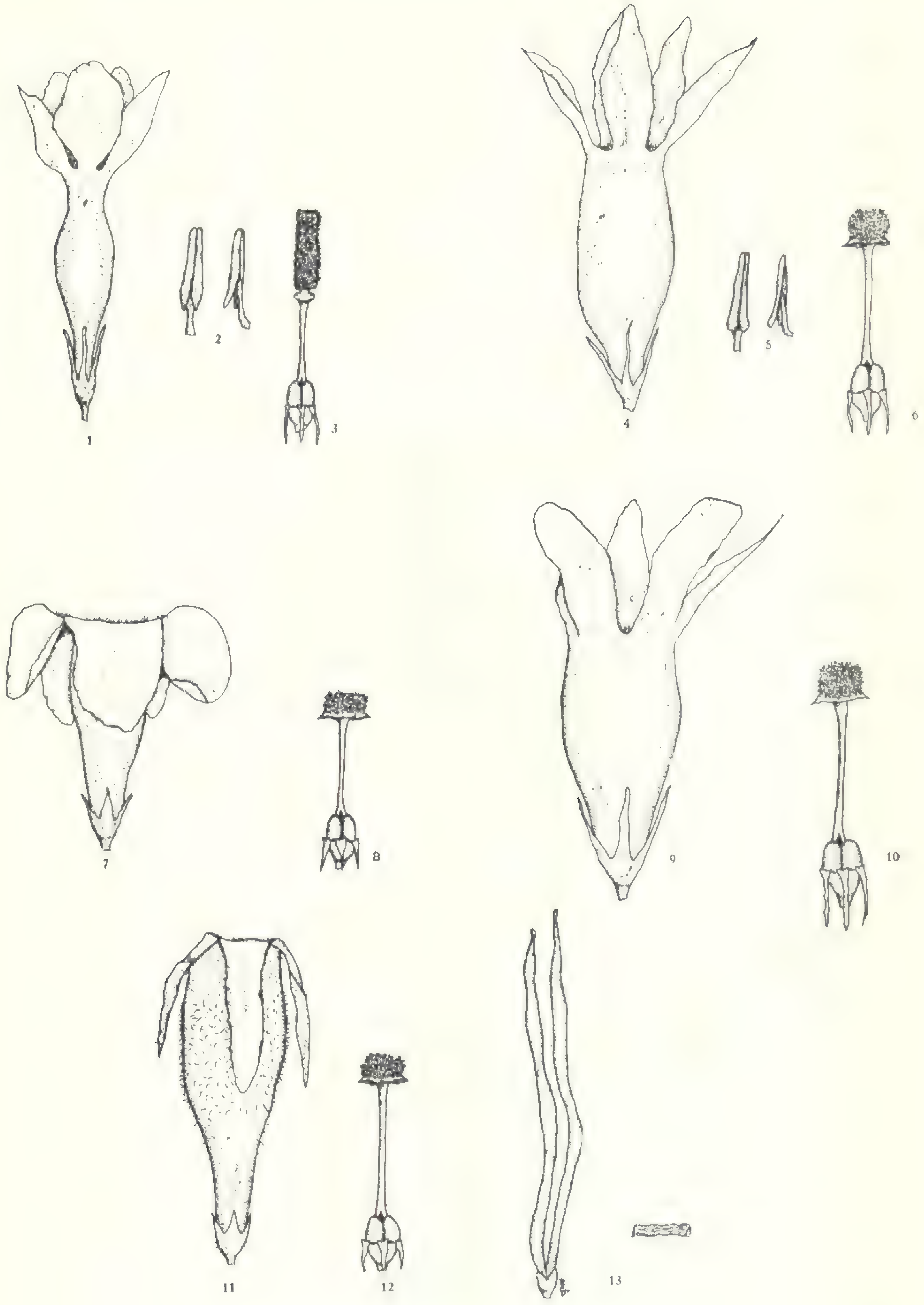
Fig. 7. Flower.
Fig. 8. Pistil.

A. elliptica (Thunb.) Roem. & Schult.

Fig. 9. Flower.
Fig. 10. Pistil.

A. Tabernaemontana Walt.

Fig. 11. Flower.
Fig. 12. Pistil.
Fig. 13. Follicles and seed. × ¼.



WOODSON—STUDIES IN APOCYNACEAE

Explanation of Plate

PLATE 52

Illustrations of the subgenus *Sphinctosiphon;* all figures × 2 except when otherwise noted.

A. Palmeri Gray.

Fig. 14. Flower.
Fig. 15. Pistil.

A. Standleyi Woodson.

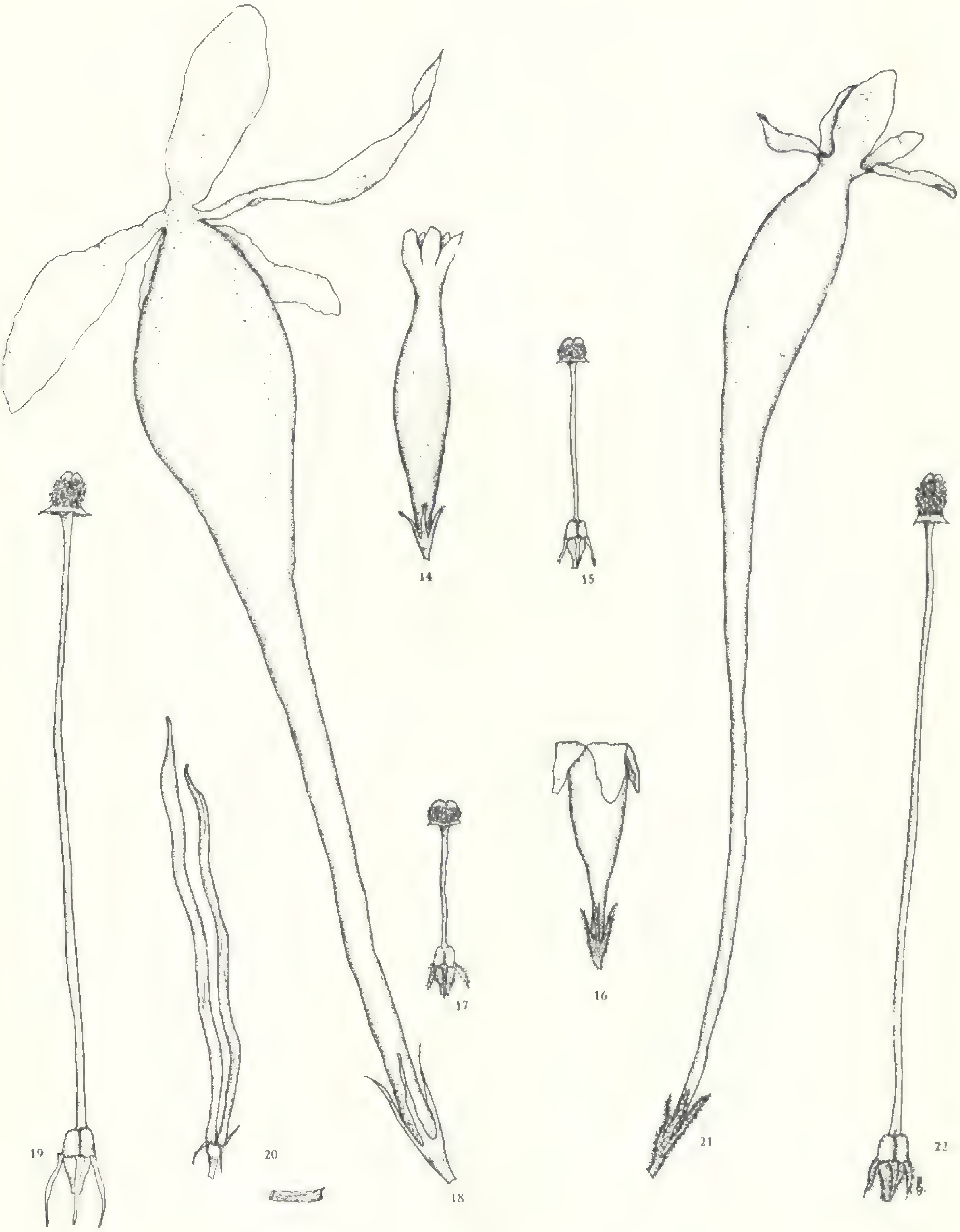
Fig. 16. Flower.
Fig. 17. Pistil.

A. longiflora Torr.

Fig. 18. Flower.
Fig. 19. Pistil.
Fig. 20. Follicles and seed. × ¼.

A. salpignantha Woodson.

Fig. 21. Flower.
Fig. 22. Pistil.



WOODSON—STUDIES IN APOCYNACEAE

Explanation of Plate

PLATE 53

Illustrations of the subgenus *Articularia;* all figures × 2 except when otherwise noted.

A. tomentosa Torr. & Frém.

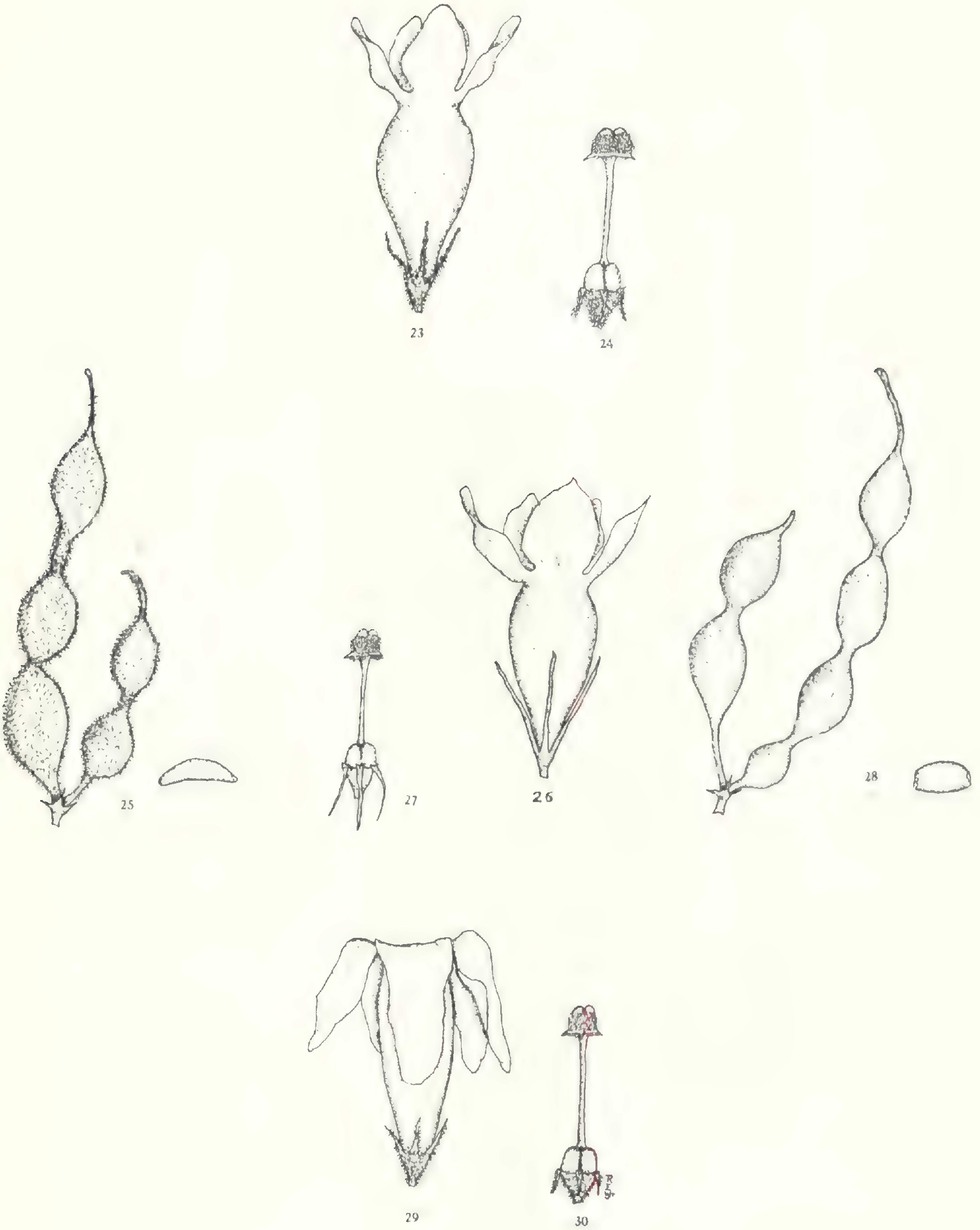
Fig. 23. Flower.
Fig. 24. Pistil.
Fig. 25. Follicles and seed. × ½.

A. brevifolia Gray.

Fig. 26. Flower.
Fig. 27. Pistil.
Fig. 28. Follicles and seed. × ½.

A. arenaria Standley.

Fig. 29. Flower.
Fig. 30. Pistil.



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